SENSORY PHYSIOLOGY AND THE RETURN OF THE ANIMAL MIND IN THE CAREER OF DONALD REDFIELD GRIFFIN, 1934-1986

by
Richard Stephen Nash

A dissertation submitted to Johns Hopkins University in conformity with the requirements for the degree of Doctor of Philosophy

Baltimore, Maryland
January, 2016

ABSTRACT

Donald Redfield Griffin (1915-2003) was an American zoologist best known for his discovery of echolocation and for his later work on animal consciousness. He was a central figure in behavioral biology and sensory physiology in the United States, and he made important contributions to the disciplinary and intellectual development of animal behavior research in the second half of the twentieth century. During his early career, he focused on the sensory physiology of animal navigation. Along with fellow Harvard graduate student Robert Galambos (1914-2010), in the late-1930s Griffin discovered the ultrasonic method of orientation in bats; in 1944 he coined the term "echolocation" to describe this phenomenon as a general method of perception. In addition to his discovery of echolocation, Griffin also made several contributions to understanding the physiological basis of bird migration and navigation, and he popularized zoologist Karl von Frisch's (1886-1982) dance language theory of the honeybee in the United States.

In 1976, Griffin surprised the scientific world by raising the question of animal consciousness, a taboo in professional science for most of the twentieth century. Although the animal mind was of central importance in post-Darwinian biology, the onset of behaviorism and mechanistic conceptions of behavior in the twentieth century relegated such inquiry to the dustbin of pseudoscience and amateurism. Beginning with his provocative book, *The Question of Animal Awareness* (1976), Griffin devoted the second phase of his career to making animal consciousness a scientifically respectable topic once again. Here again he made significant contributions to the study of animal behavior by establishing a new field of science, cognitive ethology, which is centered on

the evolutionary and comparative analysis of consciousness and cognition in animal behavior.

Doctoral Advisor: Sharon Kingsland, PhD

Thesis Committee: Daniel Todes, PhD

Robert Kargon, PhD

Angus Burgin, PhD

Nathaniel Comfort, PhD

ACKNOWLEDGMENTS

First and foremost, I am happy to thank my advisor Sharon Kingsland for her patience, criticism, and guidance of my project. Without her keen insight and close reading, I could never have completed this dissertation. Dan Todes has similarly been a magic well of intellectual support as he has challenged and inspired me to make this work my own. I also thank Angus Burgin, a tremendous influence in my approach to intellectual history and historical scholarship in general. Finally, I thank Bob Kargon and Nathaniel Comfort for their unique insights, and for their close reading and criticism of my dissertation.

My experience in the Johns Hopkins' History of Science, Technology, and Medicine program has been incredibly fulfilling and edifying. The wide-ranging intellect of the faculty and of my fellow graduate students has shown me the true meaning of scholarship and collegiality. I would like to thank in particular Graham Mooney, Larry Principe, Maria Portuondo, Bill Leslie, Yulia Frumer, and Michael Dennis for their various contributions to my intellectual development. In addition I am happy to thank Kathy Olesko for first inspiring me to study the history of science when I was a naïve undergraduate at Georgetown University.

Portions of my research were made possible by a generous grant from the Rockefeller Foundation's Archive Center. In addition, my research has been crucially assisted by several excellent archivists and librarians, including Bethany J. Antos (Rockefeller Archive Center), Christine Ruggere (JHU), Kelly Spring (JHU), Jim Stimpert (JHU), Sandra Jackson and ILL Staff (JHU), and Lawrence Marcus (Library of Congress). I am forever grateful for your knowledge and assistance.

Several graduate students and colleagues have supported me in countless ways over the past several years. It has been a great pleasure to share ideas, questions, doubts, and drinks with Ada Link, Jean-Olivier Richard, Layne Karafantis, Yixian Li, Pen Hardy, Julia Cummiskey, Eli Anders, Emily Margolis, Emilie Raymer, Matt Franco, Kirsten Moore, Simon Thode, Todd Christopher, Rex, Tom Berez, Tulley Long, Nick Radburn, and Kat Smoak. I owe a further debt of gratitude to my friends and colleagues in the JAS-Bio community. I also thank my great friends for their significant roles in my life, especially Blake and John Lennon, Tom Williams, and Kartik Venguswamy. I apologize to the many other colleagues and friends who deserve special recognition; it is unfortunate that acknowledgments are written toward the end of our intellectual endeavors, when our minds gurgle and lurch toward clarity.

Finally, I thank my family. Aimee Hess, my beautiful wife, has been a most incredibly supportive and devoted advocate. I thank her especially for generously reading several drafts, offering keen criticism and editorial advice over the duration of this long project. That Aimee has recently brought my lovely daughter Ella into this world is merely icing atop an otherwise scrumptious cake. I also thank my parents, Rick Nash and Kelly Covey, my in-laws the Hess family, and my siblings, Paige, Coleman, and Kenneth, for their encouragement and understanding as I have wandered into the bizarre world of academia.

TABLE OF CONTENTS

CHAPTER ONE
Donald Griffin and the Mechanistic Character of Twentieth-Century American Biology

Donald Redfield Griffin (1915-2003) was an American biologist and leader in advancing the study of animal behavior, sensory physiology, and physiological ecology in the mid-to-late-twentieth century. He received his Ph.D. from Harvard University in 1942 and went on to a distinguished career at Cornell University, Harvard University, and finally Rockefeller University, from which he retired in 1986. Retirement did not end his scientific research, and he continued to study the behavior of birds and mammals throughout his life. The scientific work for which he is best known was the discovery that bats navigated their environments by emitting ultrasonic sounds and analyzing their echoes, a method that Griffin dubbed "echolocation" in 1944. This work, initially conducted in collaboration with Robert Galambos (1914-2010) at Harvard, solved the centuries-old problem of how bats sensed their environments without relying on vision. Griffin also conducted important research on bird migration and homing behavior, another longstanding biological problem that had drawn the attention of many researchers. In this work he developed innovative methods to study these problems and clarified many of the key issues involved. In tandem with other ornithologists, he advanced the celestial theory of navigation by showing that many migratory species used the motion of the sun and stars to orient themselves homeward from unfamiliar territory.

Griffin's colleagues admired his research for its rigor, and for the care he took to base conclusions about animal behavior and perception on scientific evidence derived from laboratory experiments and field observations. It came as a surprise therefore when his colleagues heard him raise a formerly taboo subject – the thorny question of animal consciousness – at a scientific conference in 1975, following it up with a book in 1976, *The Question of Animal Awareness*.[1] The idea that animals possessed anything like human awareness or consciousness, although important in Darwinian biology and psychology in the nineteenth century, had long since been relegated to the dustbin of pseudoscience and amateurism. Griffin himself had been trained at Harvard to eschew anything but a mechanistic approach to behavior that avoided any reference to the animal mind. Yet thirty-five years later he was emboldened to raise this problem and to challenge his colleagues to take animal consciousness seriously as an object of scientific inquiry.

This dissertation explores how this change occurred in Griffin's thought. I will argue that, contrary to his own statements that the intellectual transition to animal consciousness was relatively abrupt, it was in fact a gradual but logical development of his increasingly sophisticated understanding of how animals navigated and perceived their environments. In reopening the problem of animal consciousness, Griffin was not departing from his earlier habit of thought but was carrying his life's work to a logical endpoint, to the seemingly strange idea that scientists needed to think harder about *what it was really like to be a bird or a bat*. By pursuing such questions, Griffin concluded that the subject of animal consciousness had to be raised for serious discussion and that scientists needed to be more open to the idea of viewing the cognitive abilities of animals in new and perhaps unexpected ways. His ideas, although controversial, helped to stimulate the new field of "cognitive ethology" which subsequently flourished as a

[1] Donald Griffin, *The Question of Animal Awareness: Evolutionary Continuity of Mental Experience* (New York: Rockefeller University Press, 1976).

subject of scientific research and philosophical discussion.[2] In part due to the force of Griffin's reputation and ideas, cognitive ethology has been a thriving area of research on animal behavior and consciousness ever since.

While charting Griffin's path leading to his reformulation of the question of animal consciousness, this dissertation also has other goals. One is to make a careful study of the long process of discovery that led Griffin to identify the phenomenon of "echolocation" when he coined the term in 1944. Commentaries on Griffin's career locate the discovery of echolocation in the late-1930s in Griffin's work with Galambos.[3] In those early studies, however, Griffin and Galambos concentrated on just one problem, how bats avoided obstacles. I will argue that we must see the discovery of "echolocation" as a longer intellectual process and that it is significant that Griffin did not coin the term until 1944, after he had ceased his work with Galambos. By this point bats were firmly on the backburner, and he had taken up his doctoral research on another topic, bird migration.

By 1944 Griffin began to understand bat behavior in a new and more general way: not only did bats use echolocation to avoid obstacles, but they also used the method for more complex interactions with their environments, such as discriminating among the different objects they encountered. It was, in short, a *general* sensory tool used by bats to acquire all kinds of information about their environments. This discovery led him back to the study of bat behavior for deeper analysis, at which point he discovered that they used

---

[2] See for example the discussion in Colin Allen and Marc Bekoff, *Species of Mind: The Philosophy and Biology of Cognitive Ethology* (Cambridge, MA: MIT Press, 1997).

[3] Eileen Crist, "Griffin, Donald Redfield," *Complete Dictionary of Scientific Biography,* Vol. 21 (Detroit: Charles Scribner's Sons, 2008), p. 177-186; Carolyn Ristau, "Donald Redfield Griffin," *Proceedings of the American Philosophical Society*, Vol. 149 (Sep. 2005): 399-411; Charles Gross, "Donald R. Griffin," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 86 (2005): 1-20; H. Raghuram and G. Marimuthu, "The Discovery of Echolocation," *Resonance*: *Journal of Science Education*, Vol. 10 (Feb. 2005): 20-32.

echolocation for such complex feats as hunting insects on the wing. As Griffin grew to appreciate just how sophisticated and general was the use of echolocation, he felt the need to coin the term and to explicate its relationship to other forms of navigation by the use of echoes (including the human use of sonar and radar). What caused him to recognize and to name "echolocation" as something new? My argument, developed in chapters 2 and 3, is that Griffin's wartime work at Harvard, and especially his work with military technologies of communication and remote sensing, was crucial to the intellectual evolution that led him to conceive of echolocation as a general mode of perception. In chapters 2 and 3 I also explore the role played by technological analogs in his analysis of bat behavior, which led him to ask new questions about echolocation.

Chapters 4 and 5 are devoted to other studies of animal behavior and navigation, including the problem of bird migration, which Griffin studied for many years, and Karl von Frisch's (1886-1982) discovery of the "dance language" of honeybees, which had a profound impact on Griffin's ideas about animal behavior and communication. His doctorate was devoted to another longstanding biological problem of great significance, the physiological basis of bird migration and navigation. Although Griffin had entered Harvard an amateur naturalist, his undergraduate and graduate education led him to seek explanations of behavior through the analysis of physiological mechanisms. This, he learned, was how one did proper science.

He conducted his doctoral work on bird navigation under physiological psychologist Karl Lashley (1890-1958), who studied the neurophysiology of rats and the homing behavior of birds, among other topics. One of the early proponents of John B. Watson's (1878-1958) behaviorism, Lashley had given up the strict brand of Watsonian behaviorism by the 1930s, but his approach to animal behavior was still firmly within the strictures of biological mechanism. For example, whereas Watson sought to reduce all behavior to simple mechanisms such as stimulus-response reactions and pure associationism, Lashley's neurophysiological study of rats and his bird research convinced him that the nature of the environmental stimulus was far more complex than a one-to-one correspondence with behavioral responses in the animal subject. In his conception of the instinctual basis of behavior, Lashley drew on concepts from Gestalt psychology to understand the ways in which animals perceived broader, more complex features and patterns within their environments.[4] Nevertheless, he held that the animal mind and consciousness remained nothing more than the immediate effects of neurophysiological processes, and should be studied as such. Lashley's approach to problems of animal behavior, therefore, consisted in identifying the sensory mechanisms and environmental cues that determined the animal's relationship to its environment. Griffin applied this same approach in his initial work on bats and birds, which established his reputation as a rigorous thinker, a skeptic when it came to explanations that extended beyond the simplest that the evidence allowed, and an authority on animal behavior.

In the 1950s, however, several new discoveries about the complexity of animal behavior caused Griffin to question the validity of restricting his interpretations to mechanistic frameworks. He found that echolocation was both a complex and general process, and that bats were able to modify the physical properties of their signals to accomplish a wide range of behaviors, including hunting insects on the wing. In addition, he became central to the popularization of zoologist Karl von Frisch's theory of the dance

---

[4] Karl Lashley, "Experimental Analysis of Instinctive Behavior," *Psychological Review*, Vol. 45, No. 6 (1938): 445-471.

language of the honeybee, one of the most significant discoveries in twentieth-century behavioral biology. Von Frisch showed that bees had an acute understanding of the temporal and spatial features of their environments, and that they were able to communicate this information through repeated "dance" movements to one another for the purposes of locating nectar and other biologically significant resources. Griffin wrote extensively about the discovery, organized a promotional tour for von Frisch at several American universities, and defended the theory against objections from Adrian Wenner (b.1928) and his behaviorist colleagues.[5]

Eventually, these discoveries about the complexity of animal behavior led Griffin to challenge what he saw as the unwarranted and unhelpful reductionism in purely mechanistic approaches in biology. As discussed in chapter 6, this transformation culminated in the 1970s when he began to tackle questions about animal consciousness and its relationship to behavior. In the final decades of his career, he established the intellectual and disciplinary foundations of a new field, "cognitive ethology," which was focused on the evolutionary and comparative analysis of animal thinking and consciousness. In a sense, this work, which took the mental continuity of humans and animals for granted, represented a return to Darwinian biology and psychology characteristic of the late-nineteenth century. The significance of Griffin's cognitive turn consisted primarily in his arguments against behaviorism and reductionism, and in his call-to-arms within the behavioral sciences to take the idea of animal consciousness as a serious object of critical inquiry.

---

[5] Tania Munz, "Of Birds and Bees: Karl von Frisch, Konrad Lorenz, and the Science of Animals, 1908-1973," (Doctoral Thesis, Princeton University, 2007); Tania Munz, "The Bee Battles: Karl von Frisch, Adrian Wenner and the Honey Bee Dance Language Controversy," *Journal of the History of Biology*, Vol. 38 (2005): 535-570.

With mixed success, he sought to place such questions within a sturdier experimental and theoretical framework, so as to avoid the charges of excessive anthropomorphism that had drawn criticism to the work of earlier Darwinians such as George John Romanes (1848-1894). While not all of Griffin's ideas were taken up, numerous biologists and psychologists were inspired by his ideas and by his challenge to take the animal mind seriously. This led to the intellectual expansion of cognitive ethology, which continues to be a thriving interdisciplinary field relying on modern techniques in neuroscience, sensory physiology, and cognitive psychology to understand the minds of animals. Despite the continuing presence of behavioristic skeptics who remain unconvinced by Griffin's arguments and by subsequent research on animal consciousness, the taboo has largely been eradicated.

In tracking Griffin's intellectual and professional growth, I also pay particular attention to the broader influence of key institutions—and especially of interdisciplinary interactions—in the evolution of his thinking about animal behavior. My analysis of the physiological character of Harvard biology during the 1930s, for example, shows how this positivistic and mechanistic climate constrained his approach to understanding and investigating animal behavior. Consistent with Jacques Loeb's (1859-1924) mechanistic conception of biology and John B. Watson's behaviorism, Harvard biologists broadly deemphasized the functional, evolutionary, and cognitive dimensions of behavior, focusing instead on physiological mechanisms as the key to understanding behavior.[6] Harvard's unique interdisciplinary climate, however, facilitated Griffin's discovery of

[6] Harvard biologists such as George Howard Parker (1864-1955) and physiologist William J. Crozier (1892-1955) sought to reduce complex behavioral phenomena to the quantifiable and measurable results of sensory mechanisms within stimulus-response frameworks. The quintessential neo-behaviorist of the postwar period, B.F. Skinner (1904-1990), received his PhD here under Crozier's reductionistic influence.

echolocation, and shaped his thinking about the sensory physiology of bats. His experimental analysis of behavior, which synthesized approaches in physiology, natural history, biophysics, and engineering, was the unique product of Harvard's workshop culture.[7] Similarly, Griffin's interdisciplinary wartime research on psychoacoustics and military technologies led him to reimagine the significance of ultrasonic perception in bats, which he came to see as a general process analogous to radar and sonar. Thus the timing of his discovery of echolocation during the war was not coincidental: wartime technologies had an important role in stimulating new thinking about animal behavior, indeed in giving Griffin a new appreciation of the surprising complexity of that behavior.

Griffin spent the second phase of his career at another key institution in the postwar behavioral sciences, the Rockefeller University. In 1965 Rockefeller president Detlev Bronk (1897-1975) recruited Griffin to strengthen the newly created behavioral sciences program. Bronk was firmly committed to the ideal of interdisciplinarity, and he sought scientists who could attack problems from a diverse range of approaches while challenging scientific convention in the process. Griffin answered the call, and in his later career at Rockefeller he came to focus intently on the problem of animal consciousness, working to convince his colleagues and critics that the animal mind was a valid scientific subject.

Reflecting on his career in the 1980s, Griffin aptly described himself as an experimental naturalist. Methodologically, he used the tools of experimental sensory

[7] In this sense, the mechanistic climate within the biology department was consistent with the various manifestations of operationism embodied in the work of Harvard physicist Percy Bridgman (1882-1961) and psychophysicist Stanley Smith Stevens (1906-1973). Historian Joel Isaac has shown how these methodologies were bound up with the pedagogical practices and the particular workshop culture of interdisciplinary science at Harvard during the middle-twentieth century. Joel Isaac, *Working Knowledge: Making the Human Sciences from Parsons to Kuhn* (Cambridge: Harvard University Press, 2012), especially p. 92-124.

physiology in order to better understand the behavior of animals in their natural environments. Much of the work on animal behavior in the United States during this period took place within the field of comparative psychology, which ran somewhat parallel to Griffin's work. American psychology in the first half of twentieth century was largely characterized by behavioristic approaches that utilized laboratory conditioning to investigate learning within a stimulus-response framework. Griffin's work, however, shared more with European ethology, as he focused primarily on the natural behavior of animals, and he was less interested in questions about learning.[8]

Griffin was a widely known and highly respected biologist in the postwar period, and I have taken a biographical approach to his intellectual and professional development. In doing so, my dissertation explores several major themes and discoveries that are crucial for understanding the new directions taken within biology and the behavioral sciences in the postwar period. Griffin's career provides an excellent window through which to view some of the most important changes in behavioral biology and in our understanding of the relationship between humans and animals.[9] My aim has been to construct a focused account of Griffin's career, rather than to write a comprehensive biography of his life in science. To this end, I analyze how Griffin's approach to

[8] On the history of ethology, see Richard Burkhardt, *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology* (Chicago: University of Chicago Press, 2005); W.H. Thorpe, *The Origins and Rise of Ethology*: *The Science of the Natural Behaviour of Animals* (London: Praeger, 1979). Neither Burkhardt nor Thorpe discusses American work on sensory physiology, which was an important area of animal behavior research.

[9] Several scholars have argued for the importance of biographical perspectives in the history of science. See for example, Thomas Hankins, "In Defence of Biography: The Use of Biography in History of Science," *History of Science*, Vol. 17, No. 1 (Mar. 1979): 1-16; Robert M. Young, "Biography: The Basic Discipline for Human Science?" *Free Associations*, Vol. 11 (1985): 108-130; Tania Munz, "Of Birds and Bees: Karl von Frisch, Konrad Lorenz, and the Science of Animals, 1908-1973," (Doctoral Thesis, Princeton University, 2007); Daniel Todes, *Ivan Pavlov: A Russian Life in Science* (Oxford: Oxford University Press, 2014).

understanding animal behavior has changed over time, and I identify the key influences that have shaped his scientific thought.

Reductionism, Mechanism, and Behaviorism: Animal Behavior in the Twentieth Century

Before giving a brief account of Griffin's early life and education, it is necessary to establish more fully the major philosophical commitments within the American behavioral sciences in the early twentieth century. In the scientific analysis of animal behavior, the foremost methodological principle was known as "Morgan's canon," which called for the rejection of unnecessary mentalistic hypotheses in behavioral explanations. British comparative psychologist Conwy Lloyd Morgan (1852-1936) formulated his canon primarily as a broad criticism of his predecessor and colleague, George John Romanes (1848-1894). Romanes, like Morgan, was a staunch Darwinian, and his goal was to explain animal behavior in terms of the evolutionary continuum from the lower organisms up to man. However, Morgan criticized Romanes' methodology for its heavy reliance on anecdotal evidence, which lacked objective rigor. He also argued that although behavior ought to be understood within the Darwinian evolutionary framework, Romanes was guilty of excessive anthropomorphism in attempting to reconcile animal behavior with human psychological states and mental processes.

Thus Morgan argued that explanations of animal behavior ought to be constructed in accordance with the principle of parsimony, using the fewest and most reductionist assumptions possible. He first articulated his canon in *An Introduction to Comparative Psychology* (1896), explaining: "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale."[10] By the turn of the century, this psychological formulation of Ockham's razor became the gold standard for biologists and psychologists, and it was epitomized in methodological commitments such as E.L. Thorndike's associationism, Jacques Loeb's mechanistic conception of biology, and John Watson's behaviorism.

Complementary to this philosophical perspective was another reductionist framework, the mechanistic conception of behavior. Largely developed in the work of German-born American physiologist Jacques Loeb (1859-1924), the mechanistic conception held that to explain animal behavior was a matter of identifying and describing the physiological mechanisms causally connecting the animal to its sensory environment. In his 1912 book, *The Mechanistic Conception of Life*, Loeb argued that all apparently psychic phenomena were merely the result of physico-chemical processes.[11] And because physiological mechanisms were the common substrate of animal life, he explained, the behavior of the higher animals, and even man, could likewise be understood mechanistically. The "animal will," Loeb argued, "was only the expression of our ignorance of the forces which prescribe to animals the direction of their apparently spontaneous movements just as unequivocally as gravity prescribes the movements of the planets."[12] Essentially, Loeb sought to reduce all explanations of behavior to a framework of stimulus-response mechanisms, which encompassed the physical and chemical forces within the external environment that wholly determined the behavior of animals.

Historian Philip J. Pauly has identified a handful of direct descendants of Loeb's mechanistic epistemology, including John Watson, Harvard physiologists George

---

[10] C. Lloyd Morgan, *An Introduction to Comparative Psychology* (London: Walter Scott, 1896), p. 53.
[11] Jacques Loeb, *The Mechanistic Conception of Life* (Chicago: University of Chicago Press, 1912).
[12] Jacques Loeb, *The Mechanistic Conception of Life*, p. 36.

Howard Parker (1864-1955) and William J. Crozier (1892-1955), and neo-behaviorist psychologist B.F. Skinner (1904-1990), who studied with Crozier at Harvard in the 1930s.[13] Sensory physiologist and zoologist George Howard Parker applied Loeb's vision to Harvard biology, where he united the formerly separate departments of zoology, botany, and general physiology into the Institute of Biology. He and Crozier, who helped create the institute, thought that it should represent the intellectual and institutional synthesis of Harvard biology, based on the Loebian ideal of physiological reduction. Beyond those individuals that he immediately influenced, Loeb's impact on early-twentieth century biology was tremendous.[14] The long shadow of Loeb is truly realized when we see how his mechanistic epistemology shaped the types of questions one could legitimately pose about animal behavior, and the approaches one took to answering such questions.

When Griffin came to Harvard in 1934 as an undergraduate and then graduate student, he entered a milieu that had been dominated by Loebian ideals of science, although the intellectual climate was by that time starting to change. Nevertheless, in fields such as sensory physiology, and particularly in places such as Harvard biology, Loeb's mechanistic vision was very much alive. Behavioral causation was still reduced to the mechanistic relationship of the animal to its environment, and the cognitive and psychic dimensions of behavior were seen as irrelevant and unscientific when it came to understanding the animal.

The last methodological principle of this reductionist triumvirate was Watson's behaviorism, which is closely related to Loeb's mechanistic view. Indeed Pauly

---

[13] Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987), p. 164-200.
[14] Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology*, p. 164-200.

characterized Watson as one of the prominent Loeb-influenced scientists of the next generation. Since Watson worked with Karl Lashley, Griffin's thesis advisor, another connection to Loebian ideals came through that line of descent. Watson formulated his "behaviorist manifesto" in 1913 when he was working with Lashley. In the manifesto he argued that the ultimate goal of a purely objective psychology was the prediction and control of behavior, and that questions concerning consciousness or mental states should be permanently jettisoned from science.[15] The rapid and nearly universal sanctioning of Watson's behaviorism among American psychologists in the decades that followed has been well documented in histories of psychology.[16] Behaviorism was based on the idea that a truly objective science of experimental psychology must reject the seemingly unknowable aspects of the subjective mind (along with methods such as introspection and the anthropomorphic analysis of anecdotal evidence). Proponents of behaviorism insisted that explanatory frameworks of behavior ought to be reduced to observable, quantifiable actions based on the stimulus-response model of conditional learning. Watson's manifesto was the most forceful articulation of that view.

During the heyday of American behaviorism from the 1920s to the 1950s, fields such as experimental sensory physiology—with no apparent need of hypotheses about animal minds or subjective states—flourished in academic biology. Research in sensory physiology paralleled approaches to animal behavior within behaviorist psychology, although scientists within the latter field were focused mainly on questions of learning

---

[15] John B. Watson, "Psychology as the Behaviorist Views It," *Psychological Review*, Vol. 20 (1913): 158-177.

[16] See for example Robert Boakes, *From Darwin to Behaviourism* (Cambridge: Cambridge University Press, 1984); Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987); Kerry Buckley, *Mechanical Man: John Broadus Watson and the Beginnings of Behaviorism* (New York: The Guilford Press, 1989); Roger Smith, *Between Mind and Nature* (London: Reaktion Books, 2013); Jamie Cohen-Cole, *The Open Mind: Cold War Politics and the Sciences of Human Nature* (Chicago: University of Chicago Press, 2014).

and conditioning in laboratory animals such as the pigeon and the white rat. Nevertheless, the scientific topics selected and their methods of analysis by sensory physiologists reflected this behavioristic intellectual climate. Even though one might be incapable of discerning the cognitive dimensions of phenomena such as bird migration, for example, the sensory physiologist had much to discover about the mechanisms involved. Broadly speaking, these areas of research included the biophysical nature of environmental cues—visual, auditory, olfactory—that provided information crucial to a bird's orientation, the comparative anatomy of sense organs, and the physiological mechanisms by which the senses operated.

For biologists interested in animal behavior, therefore, a truly comparative physiology of the senses was an indispensable aspect of their work. Once these physiological mechanisms were sufficiently understood, it was thought, more general theories might be formulated in explaining animal behavior, including questions about ecological adaptation, evolution, and development—subjects that became central in the midcentury work of European ethologists such as Konrad Lorenz (1903-1989) and Niko Tinbergen (1907-1988). Although Watson's brand of behaviorism became increasingly less popular in the postwar era, especially with the spread of Gestalt psychology and the rise of cognitive psychology in the late 1950s, one important element remained untouched.[17] Consciousness—and in particular, animal consciousness—was unscientific, and to discuss it seriously meant risking one's reputation as a serious and credible scientist.

[17] Despite its increasing unpopularity, behaviorism remained prominent in the work of psychologists such as B.F. Skinner (1904-1990), who took Watson's ideas to their most extreme by suggesting that human behavior could be predicted and controlled with great precision.

Griffin entered a Harvard environment dominated by methodological reductionism, although the climate was beginning to change with advances in biology. By the late 1930s, the simple stimulus-response mechanisms that Loeb championed began to fall out of fashion. Lashley for example showed that the causal relationships between environmental stimuli and animal behavior were much more complex than Loeb imagined them to be. But those like Lashley who were instrumental in challenging the over-simplifications of Loebian science did not abandon the basic point of view that served as a bulwark against discredited forms of anthropomorphism. This environment was quite different from Griffin's early experiences as a naturalist, and it shaped him as a scientist in profound ways. But he did not completely abandon his early interests in natural history, nor the fascination with studying animals in the wild that grew out of his early educational experiences. As we probe his later research and its evolution toward the problem of animal consciousness, it is important to keep in mind that as a young man he started out not as a Loebian, but as a keen naturalist, as the next section briefly discusses.

Donald Redfield Griffin: A Biographical Introduction

Donald Redfield Griffin was born to Mary Whitney Redfield and Henry Farrand Griffin on August 3, 1915, near Scarsdale, New York. His father ran a successful advertising agency, while his mother stayed home to care for Donald. Griffin's earliest "quasi-scientific recollections" were of the woods and fields in the rural vistas surrounding his boyhood home.[18] Wild mammals and birds were a lifelong fascination for him, and exploring nature and the behavior of animals played a central role in his

[18] Donald Griffin, "Recollections of an Experimental Naturalist," in *Leaders in the Study of Animal Behavior*, ed. Donald Dewsbury, p. 120-142 (Cranbury, NJ: Associated Universities Press, 1985), p. 121.

early development. Natural history books were also a beloved pastime. In two autobiographical memoirs, Griffin recalled that as a youth one of his favorite activities was to have his mother read aloud from Ernest Thompson Seton's fanciful anthropomorphic books on animals, and from National Geographic's *Wild Animals of North America*.[19]

In 1924, his father had the misfortune of being diagnosed with high blood pressure, and so he retired and relocated his family to peaceful Barnstable, Massachusetts.[20] From this New England wilderness near Cape Cod, Griffin's fascination with wild animals took center stage. Here he became an avid-outdoorsman and amateur naturalist, obsessed with observing, trapping, and collecting skins of the rich mammalian fauna surrounding his childhood home. His early life was thus defined by his exploration of the outdoors and by his relationship to wild animals. An only child and notably independent, Griffin was at home in nature, and he took great pleasure in his interactions with birds and mammals.

During this romantic Twainian adolescence, Griffin's education became "extraordinarily irregular." A year at the Barnstable Grammar school (1925-26) convinced his parents that he "had learned nothing except how to play craps." Perhaps more tellingly, Griffin's most vivid memory of that first and only year at the school was of a "forbidding white-haired principal [who] suddenly let fly a violent diatribe against that hideous doctrine of evolution" when in April 1926 the botanist Luther Burbank was "struck dead by the Lord because of his blasphemous advocacy of evolution." Cornish

---

[19] *Wild Animals of North America* was created from two separate articles on large and small mammals of North America from 1916 and 1918, respectively. His mother read to him so frequently, in fact, that Griffin recalled his parents' anxiety that he might never learn to read himself.
[20] Donald Griffin, "Recollections of an Experimental Naturalist," p. 122.

harangued a gathered throng of elementary students, “Do any of *you* believe your grandmother was a monkey?” According to Griffin, “my faint objections were drowned out by the chorus of horrified NOs.”[21] The degree to which he was truly a convinced Darwinian at the age of ten—as this autobiographical reflection suggests—is difficult to assess. Perhaps the appeal of casting himself a precocious evolutionist outweighed the fidelity of his memory later in life. His next two academic years (1926-28) were spent at the Tabor Academy, a small school where, when he was not otherwise reading books and periodicals on hunting such as *Fur, Fish, Game*, he spent “a great deal of time in study hall designing cages for a future fur farm.” Such distractions, he recalled, drove his father “nearly to despair.” Deciding to pull him out of school, his parents hired a private tutor to assist his father in educating him at home. Henry, an amateur historian and novelist, presided over his son’s instruction, which “was almost continually punctuated with vivid comments on the stupidity of conventional education.”[22]

Griffin’s maternal uncle Alfred C. Redfield, “another important guiding influence on [his] scientific interests,” helped to cultivate his nephew’s interest in natural history. A distinguished Harvard comparative physiologist, amateur ornithologist, and early leader at Woods Hole Oceanographic Institute, Redfield occasionally took his precocious nephew to the Boston Museum of Natural History, exposing the young naturalist to the professional side of biological inquiry. At the museum, “a whole new world of scientific books and journals” was opened to Griffin. Curators Francis Harper and Clinton V. McCoy also guided Griffin’s “clumsy efforts to become a mammalogist” by introducing him to literature on preparing skins, while simultaneously discouraging him from

[21] Donald Griffin, “Recollections of an Experimental Naturalist,” p. 121-123.
[22] Donald Griffin, “Recollections of an Experimental Naturalist,” p. 123.

becoming a professional trapper.[23] Under their influence, Griffin was led at the young age of fifteen to subscribe to the *Journal of Mammalogy*—it would remain a lifelong favorite of his.[24]

During his teenage years he became increasingly interested in bats, particularly in their seasonal migration patterns and the ways in which they moved through their environments. He spent much of his free time banding birds and bats in order to track their annual movements, ultimately tagging thousands of individuals over the course of a few years. Significantly, he became interested in the scientific practices of studying wild animals; for example, recording anatomical features of taxonomic value, and learning to chart migratory patterns for documenting a species' geographic range. As a teenager he submitted reports of his discoveries to scientific journals.[25] Evidently much of Griffin's exploration was solitary. An autodidact in many respects, he taught himself how to catch little brown bats (*myotis lucifugus*), and around 1934 he applied to the U.S. Bureau of Biological survey for a permit to use aluminum bird-bands on the bats, which he was eventually allowed to do after some initial pushback from the Bureau. He also made a name for himself in nearby neighborhoods and towns as someone who knew how to deal humanely with a bat or skunk infestation—a reputation that he maintained even late in life, as attested to by numerous such requests preserved in his personal papers.[26]

---

[23] Donald Griffin, "Recollections of an Experimental Naturalist," p. 122-123.

[24] During the 1930s the *Journal of Mammalogy* mainly published articles on mammalian systematics, geographical distribution, and migration. Articles about behavior or sensory physiology were rare.

[25] Griffin subscribed to the *Journal of Mammalogy* at the age of 15, and published five articles in it, his favorite journal, by the time he finished his undergraduate degree (1938).

[26] Griffin received written requests from people interested in eradicating bats from their attics and garages throughout his distinguished career. He took care to write thoughtful responses, urging his inquisitors that bats were mostly harmless, and encouraging them to deal with such "problems" in a humane fashion. Donald Griffin, "Recollections of an Experimental Naturalist," p. 122-124.

Worried that they had perhaps not prepared him enough for a successful profession, in 1931 Griffin's parents sent him off to the elite preparatory Phillips Andover to better his chances for a college education. "After some initial academic disasters," Griffin did "reasonably well" in algebra, French, and Latin. Biology classes were unavailable to tenth-graders, so he received informal tutoring from biology instructor Larry Shields.[27] Due to a series of "rather severe grippe infections" that spread to his inner ear, however, Griffin had to finish both tenth and eleventh grades recuperating at home.[28] After he passed the eleventh-grade college board examinations, his parents agreed to let him stay home (with his "enthusiastic concurrence") for his senior year in order to recuperate physically. Amid more "vigorous" instruction from his father, he continued exploring the outdoors, banding birds and bats, and improving his sailing skills. In addition, just before his nineteenth birthday (1934) he published his first scientific article in the *Journal of Mammalogy*, on trapping and marking bats with both a tattoo method, and his preferred method using aluminum bird-bands.[29] Henry Griffin would later write to Donald, upon his graduation from Harvard: "In spite of occasional misgivings that I had helped to make you a little too old for your years—I always

---

[27] Donald Griffin, "Recollections of an Experimental Naturalist," p. 123.

[28] There is some confusion about Griffin's time at Andover in the published biographical sketches. His NAS biographical memoir states that he left Andover before finishing his junior year, but another piece written by his colleague and friend Carolyn Ristau indicates that he graduated from Andover in 1934. Andover's web site lists Griffin as a distinguished alumnus from 1934, though that does not necessarily mean that he actually matriculated from there. In his autobiographical memoir, he indicates that his years at Andover were "interrupted by illness," and that he had to finish tenth and eleventh grades at home due to a series of colds. A useful draft of a letter that Henry Griffin wrote to a Harvard dean is a crucial piece of this puzzle. It is here that I learned about Donald's grippe, and some other recurring health and physical problems that are absent from the other published sources. Henry Griffin to Delmar Leighton, [Undated 1934, draft], Series 1, Box 5, Folder 57, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

[29] Donald Griffin, "Marking Bats," *Journal of Mammalogy*, Vol. 15, No. 3 (Aug. 1934): 202-207. Writing was also a lifelong activity begun in his teenage years. He published early, often, and late in life, and in fact his last article was remarkably accepted just four days before his death in 2003.

believed that you would justify my faith that intelligence and straight thinking wins out in the end—that the play-boys pay too heavy a price for their play in after years."[30]

In chapter two I analyze how Griffin's aptitude for intelligent straight-thinking would be shaped by the very different context of Harvard biology, where he learned what it meant to do science. The experiences at Harvard exerted a profound effect on his approach to animal behavior, and gave him the rigor that established his reputation as one of the rising stars in this field, someone very much in the Harvard mold: indeed after a stint at Cornell, Harvard decided to hire him back. But he had begun his biological training as a naturalist and one might surmise that his willingness, much later in life, to ask deeper questions about what it meant to be like a bat or a bird revealed the lingering, though now matured, interests of the natural historian.

---

[30] Henry Griffin to Donald Griffin. 19 May 1938. Rockefeller University Archives. RU RG 450G875 Series 1, Box 1, Folder 1. Griffin's educational background is also important in another respect. Later in his career, he often criticized too heavy a reliance on Ockham's razor in scientific explanations, and lamented the failure of scientists to consider creative solutions to problems. Perhaps his father's insistence on the shortcomings of conventional education, which he saw as too narrowly constricting areas of learning into specializations, influenced his son's willingness to remain open-minded to ideas that were outside the mainstream of academic thought.

CHAPTER 2
Obstacle Avoidance and the Mechanistic Conception of Bats

Introduction

Despite decades of advances in experimental zoology and physiology in the early-twentieth century, several basic questions of animal behavior remained unanswered by the 1930s. One such problem—the sensory basis of bat navigation in the dark—dated back at least to the late-eighteenth century. Whereas most nocturnal animals have large eyes adapted to capture as much light as possible, bats have tiny eyes that are ill suited for life in the dark. Complicating this problem further is the fact that bats are capable of impressive feats of navigation and orientation—swiftly threading tight passageways in deep caves, and capturing tiny insects while darting about in nearly complete darkness. The Italian naturalist Lazzaro Spallanzani (1729-1799) took an experimental approach to this problem in the 1790s, discovering that bats depended not on their eyes for navigation, but apparently on some sense related to their ears—whether it was hearing or the sensation of mechanical pressure more generally, he could not be sure. Spallanzani's experiments, which were concurrently repeated and confirmed by the Swiss naturalist Louis Jurine (1751-1819), demonstrated that while blind bats were capable of navigating the darkness and capturing insects, deafened bats were not. However, a full solution to "Spallanzani's bat problem" eluded these investigators, since bats seemed to fly in complete silence.[1] If auditory cues or hearing were necessary for navigation, then what were the cues? The problem lay dormant for most of the nineteenth century, and in fact by 1900, most naturalists apparently accepted Georges Cuvier's purely speculative

[1] For a brief history of Spallanzani's and Jurine's experiments, see Robert Galambos, "The Avoidance of Obstacles by Flying Bats: Spallanzani's Ideas (1794) and Later Theories," *Isis*, Vol. 34, No. 2 (1942): 132-140.

explanation that bats navigated via a highly sensitive membrane located on their wings, which supposedly sensed pressure changes that alerted them to the presence of obstacles while flying.[2]

The problem was finally resolved in the late 1930s when two Harvard graduate students—Donald Griffin and Robert Galambos—conducted a series of experiments using a new acoustic technology, revealing that bats navigated via the perception of echoes of ultrasonic sounds that they emitted while in flight. Further electrophysiological work by Galambos showed that indeed, bats were capable of hearing sounds in the ultrasonic range. Their discovery depended not only on bat research from prior decades, but also on elements external to experimental zoology. One such factor was the development of new acoustic technologies in the 1930s that could create, detect, and translate ultrasonic sound into the audible range of humans. The particular device that Griffin and Galambos used in their discovery was made possible by the flourishing of electro-acoustic technologies that were initially developed for submarine detection and electronic communications during the First World War. Additionally, the interdisciplinary workshop culture of Harvard science in the late-1930s encouraged the exchange of ideas, methodologies, and technologies between scientific disciplines.[3] Griffin and Galambos took advantage of this interdisciplinary climate, discussing their

---

[2] Robert Galambos wrote a useful review of the scientific literature on "Spallanzani's bat problem." Robert Galambos, "The Avoidance of Obstacles by Flying Bats: Spallanzani's Ideas (1794) and Later Theories," *Isis*, Vol. 34, No. 2 (Autumn 1942): 132-140. I accept his conclusion that Cuvier's wing-membrane hypothesis reigned supreme during most of the nineteenth century. However, I do not agree with his whiggish explanation that the solution to this problem was merely the inevitable result of increasingly progressive methods of experimentation, particularly that of physiology. Other factors, which I have highlighted in this chapter, were certainly in play.

[3] On interdisciplinarity at Harvard during this period, see: Joel Isaac, *Working Knowledge* (Cambridge: Harvard University Press, 2012). Although Isaac focuses mainly on Harvard's workshop culture and its influence on the human sciences, he identifies key interstitial bodies in the "Harvard complex" such as the Psycho-Acoustic Laboratory and the Society of Fellows, which fostered such collaborative exchanges. These particular institutions influenced Griffin's psychophysical and technological approaches to investigating the navigation of bats.

work and borrowing equipment from physicists, physicians, and engineers who were willing to assist them on solving the bat problem.

Furthermore, the particular character of Harvard biology in this period was overwhelmingly physiological, and thus encouraged approaching problems of animal behavior through methods firmly grounded in experimental sensory physiology. In the case of bat navigation, this entailed a careful analysis of the senses that formed the basis of navigation. From such a perspective, Griffin viewed the basis of bat navigation as constituted by particular sensory mechanisms that could be isolated and quantified with great precision. This mechanistic approach sought to identify the relationship between specific environmental cues and the sensory anatomy and physiology that mediated such stimuli in determining the bat's navigational behavior. Thus to explain behavior such as the bat's entailed describing the physiological mechanisms that undergirded it, ignoring concepts such as instinct, intelligence, awareness, or other mental faculties. A secondary consequence of the mechanistic approach to problems of animal behavior was that sensory mechanisms could be understood in terms of technological analogs designed for similar functions in human activities. This, as we will see in future chapters, would play an important role in Griffin's shifting understanding of bat navigation.

This chapter is divided into three parts. I first analyze Griffin's undergraduate education in Harvard's physiologically oriented biology department, demonstrating how such a context influenced his approach to animal behavior. Next, I analyze several lines of research on Spallanzani's "bat problem" in the early-twentieth century, which preceded Griffin's and Galambos's work. Finally, I explain the obstacle avoidance experiments that they conducted between 1938 and 1940, which ultimately solved the problem of bat orientation. In the following chapter, I examine Griffin's wartime research at Harvard, which helped to transform his conception of both bat echolocation and sensory physiology more generally after the war. Griffin's postwar conception of echolocation and the corresponding research paths that he pursued illustrate how metaphorical reasoning—connecting the biological and technological spheres—shaped his scientific ideas. Thus I argue that the discovery of echolocation was not a singular moment or insight, nor was it the inevitable result of progressive experimentation in the field of sensory physiology. Rather, the "discovery" was actually a gradual process, transformed by elements external to routine experimentation and scientific practice, that took place over the course of several years.

Donald Griffin and Harvard Biology in the 1930s

With a rather unorthodox academic mosaic in his pre-collegiate education, Griffin was nevertheless admitted in 1934 to Harvard, where he would spend most of the next three decades. As an undergraduate he focused intensely on biology and studied bat physiology in several research projects that complemented his coursework. His transcript attests to his father's successful instruction, as Griffin performed well on the entrance exams. As he later recalled, a lack of high school science "did not seem a serious handicap except that it was quite late before I learned even the rudiments of chemistry and physics."[4] Griffin took courses mainly in biology, supplemented by four courses in chemistry, a physics course in his sophomore and junior years, and a psychology course

[4] Donald Griffin, "Recollections of an Experimental Naturalist," in *Leaders in the Study of Animal Behavior*, ed. Donald Dewsbury, p. 120-142 (Cranbury, NJ: Associated Universities Press, 1985), p. 125.

taught by E.G. Boring his junior year.[5] He passed the general examinations in biology in May of his senior year (1938), and performed well enough to be excused from taking the final examinations in biology and chemistry courses in his last semester.[6] Receiving mostly A's and B's, Griffin was elected to Phi Beta Kappa in June of 1938 upon receiving his B.S. in biology.[7]

Griffin's undergraduate career coincided with some important structural and intellectual transformations within Harvard's biology department. Between the mid-1920s and 1930s, the disciplines of general physiology, botany, and zoology were gradually consolidated into a unified department. Simultaneous to these changes, the character of Harvard biology began to lean more heavily toward experimental physiology. Physiology, traditionally located within the medical school, had only recently been established in 1924 as a department under the division of biology in the Faculty of Arts and Sciences.[8] With the encouragement of zoology chair George Howard Parker—a physiological zoologist—and the newly hired chair William J. Crozier, the department flourished.[9] But Parker had even grander changes in mind, and along with Harvard president A. Lawrence Lowell, he envisioned the reorganization of the biological disciplines at Harvard into a unified "Institute of Biology." The Institute constituted both a physical space and an interdisciplinary ideal—it would not only house the zoological,

---

[5] E.G. Boring's course was "Psychology I," an introductory course that surveyed the history of psychology from the ancients to the present.
[6] E.S. Castle to Donald Griffin. May 12, 1938, Series 1, Box 5, Folder 57, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[7] Harvard College [Unofficial Transcript], Series 1, Box 5, Folder 57, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[8] For an institutional chronology of Harvard biology, see: Clark A. Elliott, "Chronological Overview of Harvard Science (1636-1945) [Appendix 2]," in *Science at Harvard University*, eds. Clark A. Elliott and Margaret W. Rossiter, p. 331-360 (Bethlehem: Lehigh University Press, 1992).
[9] On Parker, see: Alfred Shermer Romer, "[Biographical Memoir of] George Howard Parker (1864-1955)," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 53 (1967): 357-390.

botanical, and physiological laboratories under the same roof, but would also create a research-oriented "nucleus" of cooperative biological work with the goal of discovering "new truth in the realm of organic nature."[10] Thanks to a $3 million contribution from the Rockefeller Foundation, the massive, five-story laboratory complex was opened in 1931.[11] The final piece fell into place in 1934, when recently appointed Harvard president James Conant continued the work of his predecessor in consolidating the faculties of zoology, botany, and physiology into a unified department of biology, headed by a single chair.[12] As a result, by the mid-1930s the biology department—with the exception of the Museum of Comparative Zoology, a separate but related institution—leaned heavily toward physiology.

In addition to institutional changes, the intellectual axis of Harvard biology was also shifting. In 1925 Parker hired William J. Crozier—a physiologically oriented zoologist with grand ideas about the "Loebian" future of biology. As Philip J. Pauly has shown, Crozier was adamant and aggressive in his belief that the functional studies of general physiology were the key to achieving Loeb's vision of reformulating biology from a natural science to an engineering one.[13] Loeb championed a mechanistic view of biology in general, and of animal behavior in particular, and Crozier's hiring signaled the beginning of a decade-long trend toward creating a physiologically oriented biology

[10] George H. Parker, "The New Harvard Biological Laboratories," *Science*, Vol. 76, No. 1964 (Aug. 1932): 160.
[11] The building itself was more commonly referred to simply as the "Biological Laboratories."
[12] Conant's predecessor, A. Lawrence Lowell, had worked with George Howard Parker and William Crozier in the 1920s to establish a new "Institute of Biology," funded mainly by the Rockefeller Foundation.
[13] Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987), p. 183-185, 199.

faculty.[14] Along with Parker and Lowell, Crozier also oversaw the construction of the Institute of Biology, making certain "that general physiology shared space on an equal footing with the long-established departments of zoology and botany."[15] In addition to these changes, the biology faculty became academically inbred in the 1930s, thus shielding its physiological bent from external influence. According to historians Morton and Phyllis Keller, between 1930 and 1938 only home-grown Harvard PhDs received permanent appointments in the department.[16]

Donald Griffin's uncle Alfred Redfield served as the first chair of the new department in 1934. A comparative physiologist who migrated from the Medical School, Redfield summarily resigned after only one year, citing his frustration over academic politics—specifically with Harvard president James Conant's meddling in departmental affairs.[17] Redfield's chairmanship was followed in 1935 by that of another physiologist, Alden B. Dawson, who specialized in cell biology and morphological physiology. After Dawson resigned in 1940, Edward S. Castle, a botanist and associate professor of physiology became chair, despite earlier efforts by Conant to deny him a permanent professorship in 1939.[18] Other faculty during this period included the aforementioned George Howard Parker (sensory physiology), William "Cap" Weston (mycology), John H. Welsh (invertebrate physiology), Theodore James Blanchard Stier (metabolic physiology), Ralph Wetmore (botany), George Wald (sensory physiology), Jeffries

[14] Behaviorist psychologist B.F. Skinner (1904-1990) conducted his doctoral work under Crozier's guidance at Harvard between 1928 and 1931.
[15] Philip Pauly, *Controlling Life*, p. 185.
[16] Morton Keller and Phyllis Keller, *Making Harvard Modern: The Rise of America's University* (Oxford: Oxford University Press, 2001), p. 99.
[17] Keller and Keller, *Making Harvard Modern*, p. 99.
[18] Keller and Keller, *Making Harvard Modern*, p. 100. Conant's exact reasoning is unclear in Keller and Keller, but it is implied that Conant was generally unimpressed by much of the biology faculty, and had hoped to bring in some more prestigious names while simultaneously quashing the department's tendency to promote from within.

Wyman (physical chemistry, physiology), Charles Thomas Brues (entomology), Leigh Hoadley (embryology), and Alfred Romer (evolutionary biology, paleontology).[19] Hallowell Davis (sensory physiology) and Alexander Forbes (sensory physiology), professors at Harvard's medical school, also collaborated frequently with the biology department and occasionally advised doctoral research.

By the mid-1930s, then, as Griffin recalled, "physiology was the order of the day, and animal behavior was considered too vague for serious scientists."[20] As an undergraduate, therefore, he learned to modify his approach to studying animals from a naturalist's perspective—observing, collecting, and recording their movements in the wild—to a physiological one. Despite Conant's efforts to limit the Harvard tutorial plan so that professors could focus more on their own research, the biology department still took tutoring seriously. Griffin's instructor was physical chemist Jeffries Wyman. Along with Griffin's uncle Alfred Redfield, Wyman shepherded Griffin through his transition to Harvard and taught him to think more like a physiologist when it came to zoological inquiry. As Griffin described it, physiology at Harvard was understood as an essentially comparative field, "one subject and not readily divisible along phylogenetic lines."[21] In order to understand the migratory behavior of bats, for example, one must know much more than the structure, speed, and timing of annual migrations from their hibernating caves to summer breeding haunts. To address such a problem, a Harvard biology student

---

[19] Hoadley and Lashley each taught one half of "Biology 20" in 1939-40. Alfred Romer was appointed in the MCZ but was closely affiliated with the biology department.

[20] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 73. Among the few that took animal behavior seriously was director of the Museum of Comparative Zoology (MCZ), Glover Allen—also a bat expert and a friendly mentor to Griffin from the time before he enrolled at Harvard. The MCZ was not officially divorced administratively from the biology department until 1939, although the institutions were effectively separate before then. Keller and Keller, *Making Harvard Modern*, p. 99-102.

[21] Donald Griffin, "Recollections of an Experimental Naturalist," in *Leaders in the Study of Animal Behavior*, ed. Donald Dewsbury, p. 120-142 (Cranbury, NJ: Associated Universities Press, 1985), p. 134.

in the 1930s ought to study the comparative physiology of mammals, including physiological mechanisms that controlled diurnal periodicity.[22]

Under these influences, Griffin explained, "physiology came to seem to me and most of my fellow students the substantial science of the future. Bat banding, mammalian systematics, or similar things were old-fashioned natural history, we were led to recognize—suitable for amateur dilettantes, perhaps, but not serious science suitable for one aspiring to a professional academic career."[23] Another biology undergraduate during the mid-1930s, Vincent Dethier, was overtly critical of the character of the department when recalling his time there. Although he too would later become a distinguished sensory physiologist, Dethier's early experiences in the biology department made him queasy: "the inexhaustible vocabulary of technical terms that riddle biology […], the welter of details to the exclusion, or subordination, of principles and generalizations […] To one whose prior experience had been with living organisms and who was attracted to nature by the *behavior* of organisms and the beauty and mystery of the living world, these were bitter pills to swallow."[24]

Amid this intellectual environment Griffin learned to examine animal behavior through a mechanistic framework. The long shadow of Loeb's mechanistic epistemology pushed biological inquiry toward what historian Philip J. Pauly has described as

---

[22] These would later be termed "circadian rhythms" and then generalized to the "biological clock."
[23] Donald Griffin, "Recollections of an Experimental Naturalist," p. 126. Griffin's graduate courses included Biology 25 (embryology); Biology 11a (genetics); Biology 18 (phylogeny of flowering plants); Biology 29 (invertebrate zoology), Biology 31 (cell physiology); Psychology 111 (survey); Psychology 10a (quantitative methods) and Psychology 6a (physiological psychology). In order to graduate, Griffin was also required to qualify in comparative psychology "with special reference to studies of behavior." O.E. Sandusky to Donald Griffin, 9 June 1939, Series 1, Box 5, Folder 57, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[24] Emphasis in original. Vincent G. Dethier, "Curiosity, Milieu, and Era," in *Studying Animal Behavior: Autobiographies of the Founders*, ed. Donald Dewsbury, p. 42-67 (Chicago: University of Chicago Press, 1989), p. 46. Dethier stayed at Harvard for his PhD, which he received in 1939.

explaining “the visible by imagining mechanical processes occurring on a more microscopic level.”[25] Animals were assumed to be machine-like, and their behavior was understood with reference to the specific physiological mechanisms that were triggered by corresponding environmental stimuli. With respect to the study of animal behavior in general, this biological outlook was easily compatible with and reinforced the behaviorist paradigm in American comparative psychology. Griffin thus came to consider himself not merely a zoologist but “primarily a physiologist,” focused on “mechanistic explanations of animal behavior.”[26] Recalling his graduate work on bird migration, for example, Griffin explained that his generation of young biologists at Harvard became convinced that nearly all homing behavior “could be accounted for without assuming that birds had any ability to choose the correct homeward direction when released in unfamiliar territory.” This conclusion, “which in retrospect seems so narrowly overconservative, was very much in keeping with the basic ideas on which I had been brought up in the biology and psychology department at Harvard in the 1930s. Everything that animals did must be explained on the sort of very simple basis characteristic of Jacques Loeb’s theories of tropisms.”[27] Although he would later forswear that perspective, Griffin’s intellectual development in his years at Harvard was shaped by the methodological assumption that animal behavior ought to be understood mechanistically and through the rubric of behavioristic explanations.

One of his undergraduate research projects illustrates how this perspective shaped the kinds of questions Griffin would pose about animal behavior, as well as the sort of conclusions he considered appropriate. In his junior year under professor John H.

---

[25] Philip Pauly, *Controlling Life*, p. 146.
[26] Donald Griffin, “Recollections of an Experimental Naturalist,” p. 137.
[27] Donald Griffin, “Recollections of an Experimental Naturalist,” p. 135.

Welsh—supervisor of undergraduate laboratory work—Griffin undertook the study of endogenous activity rhythms in several invertebrates, before moving up the phylogenetic scale to examine the circadian rhythms in little brown bats (*Myotis lucifugus*).[28] On the basis of Loebian mechanisms, it was thought, explanations of insect behavior should not differ in kind from those of the "higher" mammals; one needed simply to isolate the appropriate environmental stimulus and its physiological correlate in the response mechanism.[29] In these experiments we see the first explicit signs of Griffin's transition from a natural historical to a physiological approach in the study of animals.

Returning to Harvard in the fall of 1936, Griffin brought with him three little brown bats—along with experiential knowledge of their natural behavior—that were captured at the end of his banding activities that summer. Curious as to how bats hibernating in deep caves coordinated their activity according to diurnal periodicity, Griffin and Welsh found that when the bats were exposed to constant darkness in the laboratory, their activity rhythms nevertheless remained "in phase" with the day-night cycle outside. This was interesting, since it seemed to imply that some internal, clockwork mechanism was more important for regulating behavior than an external stimulus such as sunlight. While the bats therefore showed a form of endogenous activity rhythm, Griffin and Welsh also discovered that feeding times could influence that natural cycle—one bat, for example, began its 24-hour cycles according to when Griffin administered by hand its daily provision of mealworms.[30] Curiously, the cycles of the

[28] John Welsh was heavily influenced by the eminent Harvard physiologist George Howard Parker, who championed Loeb's mechanistic vision of biology.
[29] They published these results in Griffin's preferred bulletin, the *Journal of Mammalogy.* Donald Griffin and John Welsh, "Activity Rhythms in Bats under Constant External Conditions," *Journal of Mammalogy*, Vol. 18, No. 3 (Aug. 1937): 337-342.
[30] Bats are notoriously difficult to keep adequately nourished while in captivity, and here Griffin explained that he was forced to hand-feed them live mealworms in order to coax them into eating.

other two bats remained in phase with the day-night cycle regardless of when they were fed. Griffin and Welsh concluded that this activity coordination entailed a "cyclic internal process—involving perhaps the nervous or endocrine systems or both." Functioning as an auxiliary to the senses, this process could be further "emphasized by the experience of darkness and daylight."[31]

While they were unsure of the details, Griffin and Welsh were nevertheless convinced that they had found evidence of a clockwork physiological mechanism that was subject to external influence. Such a mechanism—what we today refer to as the biological clock—was seemingly at odds with the stimulus-response explanations demanded by Loebian tropisms. Nevertheless, it was still assumed to be mechanistic in nature, even if the typical framework of stimulus-response was incapable of resolving its complexity. Perhaps Griffin would have pursued this line of inquiry into endogenous activity rhythms further had he not made an even more surprising discovery a few months later.

Spallanzani's Bat Problem: Obstacle Avoidance in Bats

Spallanzani's so-called "bat problem" dated to the late-eighteenth century, and a solution had been intriguingly hinted at several times over the course of its 150 year history. In the 1790s Spallanzani and subsequently the Swiss naturalist Louis Jurine performed a series of experiments with deaf and blind bats that suggested that hearing—or some other function performed by the inner ears—was necessary for obstacle

[31] Donald Griffin and John Welsh, "Activity Rhythms in Bats under Constant External Conditions," p. 341.

avoidance in flight.[32] However, because bats flew in nearly complete silence, many naturalists remained uncertain as to what auditory or physical cues might be involved. During most of the nineteenth century, the auditory solution suggested by Spallanzani and Jurine was rejected in favor of Cuvier's tactile hypothesis, which held that bats sensed obstacles in flight via an extremely sensitive membrane that covered their wings. Cuvier's hypothesis, despite being widely accepted, was never demonstrated experimentally. Further study by several naturalists and physiologists in the early-twentieth century once again suggested that the ears of bats played the crucial role in obstacle avoidance. The sensory basis of obstacle avoidance remained an open question by the late-1930s, but one that was ripe for study within the expanding field of sensory physiology.

In early 1938, Griffin was urged by a few colleagues to meet with the distinguished professor of physics George Washington Pierce, who had invented a unique apparatus that could detect, produce, and analyze what were then known as "supersonic" sounds—that is, sounds with frequencies above the upper limit of human hearing (approximately 20,000 cycles per second, or 20kHz).[33] This sophisticated device,

---

[32] Although Jurine based his experiments on Spallanzani's, their research was independent, not collaborative.

[33] Griffin recalled that two colleagues in particular encouraged him to visit Pierce. One was James Fisk, a Harvard Society Fellow who had just received his PhD in quantum physics from MIT. At the time Fisk was beginning what would become a distinguished career in radar research. In 1940 he was hired to improve radar technology by Bell Labs, where he eventually served as president from 1959-1973. The other was Talbot Waterman, a Harvard graduate student researching the sensory physiology and neurobiology of crustaceans. Waterman, also a member of the Society of Fellows, would go on to apply "his wartime experience with polarizing gunsights to make an underwater hand-held polarizer that could be used to measure underwater polarization patterns" necessary for arthropod orientation. On Waterman's career, see: T. W. Cronin, J. Marshall and M. F. Wehling, "Talbot H. Waterman," *Philosophical Transactions of the Royal Society B*, Vol. 366, No. 1565 (Mar. 2011): 617-618.

conceived and built by Pierce, also translated high-frequency tones into audible sound.[34] A naturalist at heart, during his summer vacations Pierce had become interested in applying his expertise in physical acoustics to the analysis of insect songs in his gardens. He and his research assistant Vincent Dethier—a biology graduate student with a budding interest in sensory physiology—brought these studies into the laboratory, where they had been using the instrument to study the high-frequency noises produced by grasshoppers and other insects.[35]

After some initial hesitation, Griffin brought a cage of bats into Pierce's office as an exploratory measure.[36] Both Griffin and Pierce were almost certainly aware of some previous experimental work on obstacle avoidance in bats, including that of naturalist Walter Louis Hahn. In a series of experiments performed in 1907, Hahn had shown that neither vision, tactile membranes on the skin, nor the external ear anatomy were necessary for bats to avoid obstacles in flight.[37] Like Spallanzani before him, Hahn suspected that the inner ear played a crucial role in obstacle avoidance. However, because bats were almost entirely silent in flight, Hahn concluded that they avoided obstacles not

---

[34] For a description of Pierce's device, see: Atherton Noyes, Jr. and G.W. Pierce, "Apparatus for Acoustic Research in the Supersonic Frequency Range," *Journal of the Acoustic Society of America*, Vol. 9 (Jan. 1938): 205-211.

[35] The fact that Pierce, a professor of physics, was working with Dethier, a biology graduate student, is a testament to the spirit of interdisciplinarity encouraged by the biology department in the 1930s.

[36] In a memoir Griffin explained that it "took a considerable effort during the winter of 1936-37 [sic] to bring myself to call on the distinguished physics professor," due to his poor performance (C+) in Oldenberg's atomic physics course. Once he did, he found "Pierce a jolly fellow who was delighted to find someone who knew one end of a bat from the other." Donald Griffin, "Recollections of an Experimental Naturalist," p. 127. There is some confusion as to whether Griffin first approached Pierce in the winter of 1936-37, or 1937-38. I believe Griffin is mistaken in his autobiographical memoir, and that he actually visited Pierce in the winter of 1937-38. Their findings were published in November of 1938, and Griffin has described elsewhere their experiments were performed within a few months of that initial meeting. Donald Griffin, *Listening in the Dark: The Acoustic Orientation of Bats and Men* (New Haven: Yale University Press, 1958), p. 66-69; Donald Griffin, *Echoes of Bats and Men* (Garden City: Anchor Books, 1959), p. 29; Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 74.

[37] Walter Louis Hahn, "Some Habits and Sensory Adaptations of Cave-Inhabiting Bats II," *Biological Bulletin*, Vol. 15, No. 4 (Sep. 1908): 165-193.

by virtue of acoustic orientation, but through the mechanical sensation of atmospheric compression by a specialized organ in the inner ear.

Hahn's 1907 experiments drew on Spallanzani's much earlier work, but in his newer experiments he tested four explanations of the sensory basis of obstacle avoidance using quantitative metrics, evaluating the performance of bats under controlled experimental conditions.[38] In his experimental design, Hahn divided a large room in half by tightly stringing iron wires (black in color, about one millimeter in diameter) from the rafters to floor, spaced unevenly, but on average about eleven inches apart. He then sorted his 47 bats into four experimental groups and calculated how frequently the bats in each group were successful in avoiding the wires as they flew from one side of the room to the other.[39] Hahn observed each bat perform 50 trials, which consisted of passing through the wires from one side of the room to the other, or nearly approaching a wire before dodging it. In 2,350 total trials, normal bats struck wires about 25% of the time on average, although the ability varied substantially by individual.

In order to isolate the senses, Hahn employed four kinds of "mutilation." To rule-out vision, he covered the eyes of 12 bats with lampblack (soot) and glue, taking care that it had hardened enough so that they were unable to remove it with their claws—a difficulty that Griffin and Galambos would also have to contend with in their experiments. In 600 trials these 'blinded' bats hit the wires only 21.7% of the time. Curiously, the same group had struck the wires 23.6% of the time under normal

[38] Spallanzani's analysis was more qualitative, providing descriptive accounts of his results rather than quantifying the effects of sensory mutilations on bat flight. Also, Spallanzani gravely injured his bats by cutting out their eyes and by using a hot wire to blind them, which disrupted in general their ability to fly normally because of injury.

[39] Hahn used a mixture of Easter pipistrelles (*Perimyotis subflavus*), Western small-footed bats (*Myotis subulatus*), and little brown bats (*Myotis lucifugus*).

conditions—thus, they actually performed better when blinded.[40] In a second group consisting of 11 bats, Hahn surgically removed the external ear anatomy and tragi—small flaps that project posteriorly over the ear canal—in order to determine if they played a role in obstacle avoidance. These bats struck the wires in 31.7% of their trials, versus a 24.4% hit-rate before the amputations.[41] However, the 7% increase in collisions was largely due to the poor performance of a single bat that was injured on the operating table. Excluding the injured bat brought the hit-rate down to 23.2%, thus demonstrating that the presence of the external ear anatomy was not crucial for obstacle avoidance. In a third group, Hahn isolated the role of the inner ear. When the external auditory meatus (ear canal) was blocked by plaster of Paris, 16 of Hahn's bats showed a substantial impairment in their ability to avoid collisions. The hit-rate of these bats increased from 25.2% to 66%. Hahn interpreted the results as showing that the plaster had prevented atmospheric vibrations from reaching "the sensory cells of the internal ear." He therefore concluded that the perception of the wires by normal bats was most probably due to "the condensation of the air between the flying bat and the solid body that it is approaching," and that it was "not so difficult to imagine that condensation of the air so slight as to be imperceptible to the human ear will arouse sensations on the auditory end organs of the bat."[42] With the fourth group, Hahn set out to test Cuvier's so-called "tactile theory,"

[40] When Griffin and Galambos modified and repeated these experiments in 1939, their "blind" bats similarly performed better than they had under normal conditions. Griffin was never able to explain this curious fact.

[41] In the amputated ears group, Hahn used a mix of five little brown bats (*Myotis lucifugus*) and six eastern pipistrelles (*Perimyotis subflavus*).

[42] As part of this discussion, Hahn warned against drawing conclusions about what cognitive implications that obstacle avoidance via hearing had for the mental life of bats. "It is necessary to bear in mind in discussing the senses of the lower animals that it is impossible to form any adequate conception of the sensations and mental life of the lower animals on the basis of our own. If a piano recital is incomprehensible to a Hottentot, or a snake dance to a cultured Caucasian, how much less can either hope to understand the perceptions aroused in the brain of a hound that scents a fox, or the mental processes of a

which held that obstacle avoidance was due to the perception of atmospheric changes by tiny hairs on the wing membranes. To rule this out, Hahn slathered the bats with a thick coat of vaseline, which he assumed would render the hairs "less sensitive to slight stimulation."[43] The hit-rate for this final group also increased from 26.1% under normal conditions to 36.1% with the vaseline coatings, which seemed to lend some credence to the tactile theory. However, Hahn inferred that the layer of vaseline had made flying significantly more difficult for the bats, and he therefore concluded that although the "organs of touch" were valuable in obstacle avoidance, they were not nearly as valuable as the "auditory organs."[44]

A few months later in the summer of 1907, Hahn decided to test whether different sensory mutilations made bats more or less likely to collide directly with obstacles ("hits") or merely to brush them with their wings ("touches"). To determine this, he performed additional experiments using a modified setup, with slightly larger (15 millimeters) white cotton strips that were evenly spaced as opposed to the irregularly spaced wires. He found that even bats with unobstructed ear canals frequently had difficulty avoiding objects entirely, but they were much less likely to strike an object directly than they were to brush it with their wings. He next tested the ability of bats to form what animal psychologists termed "associations," thinking that these might aid bats more generally in obstacle avoidance. Hahn found that bats readily formed auditory associations (between specific sounds and feeding times for example), but failed to form

---

bat as he circles among the tree tops in pursuit of insects." Walter Hahn, "Sensory Adaptations of Bats," p. 173.

[43] Walter Hahn, "Sensory Adaptations of Bats," p. 173.

[44] Walter Hahn, "Sensory Adaptations of Bats," p. 174.

visual, tactile, and gustatory associations. Thus he concluded that the auditory organs played the most important role in the ability of bats to avoid obstacles.

The fact that the inner ear seemed crucial to obstacle avoidance, coupled with the near absence of sound in their flight, led Hahn to suggest that bats probably perceived obstacles through a sensory organ in the internal ear that detected "the condensation of the atmosphere between the moving animal and the object it is approaching."[45] Hahn had evidently identified pressure waves as key to obstacle avoidance, but he conceived the bats' ability to perceive them as more of a mechanical than an acoustic sense. Thus the sensory function was not synonymous with hearing: "bats do perceive objects that they are approaching by senses other than sight or hearing as usually understood. The most important sense organs for the perception of objects are in the internal ear."[46] Nevertheless, the evidence for acoustic associations was strongly suggestive of the important role that hearing played in bat behavior. He therefore concluded that these associations also aided bats in obstacle avoidance, and suggested that bats possessed a "sixth sense, that of direction," which was based on acoustic information and was further strengthened by the associative memory of the bat's surroundings.

Griffin probably first learned of Hahn's analysis from Glover M. Allen (1879-1942), a bat expert and curator of mammals at Harvard's Museum of Comparative Zoology.[47] In his magnum opus, *Bats* (1939), Allen dedicated a few pages to the

---

[45] Walter Hahn, "Sensory Adaptations of Bats," p. 188-191.
[46] Walter Hahn, "Sensory Adaptations of Bats," p. 176.
[47] I have found no direct evidence indicating when Allen learned about Hahn's work. However, given the fact that Allen studied and wrote about bats throughout his career (publishing on them as early as 1922), and the fact that Hahn's work was published by a major journal (*Biological Bulletin*) in 1908, it is reasonable to conclude that Allen probably learned about it within a few years of its publication. Certainly by the 1930s Allen would have been familiar with it, as he began constructing his magnum opus, *Bats* (published in 1939). Griffin was also interested in bats from a young age and had corresponded with Allen

discussion of obstacle avoidance.[48] While he mostly accepted Hahn's explanation of the problem, Allen was more definitive in stating what he thought constituted the true sensory basis of obstacle avoidance: "Evidently the internal ear, with its acute sense of hearing, is a main factor, not only in helping bats to avoid obstacles, but also in aiding them to hear the hum of a passing insect. No doubt it is the echo of vibrations set in motion by air currents that they really perceive."[49] Thus unlike Hahn, Allen thought that the sensory function was acoustic, not merely mechanical; that is, rather than sensing atmospheric compression via its mechanical effects on a specialized sensory organ, bats actually heard—in the traditional sense—atmospheric vibrations. He further disagreed with Hahn in claiming that it was the *echoes* of those atmospheric vibrations that bats perceived. However, Allen failed to address the heart of the matter—if bats used the reflection of sounds to avoid collisions, as he assumed, why were their flights unaccompanied by audible sound?[50]

It is important to emphasize that Hahn and Allen understood this sensory function as a fairly simple and limited ability, regardless of whether it entailed acoustic (hearing) or mechanical (pressure/tactile) sensations in the inner ear. They both considered obstacle avoidance to be a kind of crude collision warning system, rather than a general mode of

---

a few years before he became a Harvard undergraduate. He may have known about Hahn's work before even coming to Harvard, but he did not become interested in obstacle avoidance until about 1938.

[48] Glover Allen, *Bats* (Cambridge: Harvard University Press, 1939; reprinted by Dover, 2004).

[49] Glover Allen, *Bats,* p. 134-136. Although not published until 1939, Allen's expansive monograph was evidently the result of several years of work. I am not sure when he came to the conclusion that bats avoided obstacles due to the perception of echoes, but that idea was first proposed in 1920 by British physiologist Hamilton Hartridge. Allen, however, does not cite Hartridge's work.

[50] Although his book was published in 1939, his section on obstacle avoidance had probably not been updated since at least 1938. If it had, Allen surely would have mentioned Griffin's and Pierce's discovery in early 1938 that bats emitted sounds above the range of human hearing. However, because Griffin and Pierce concluded that these calls were probably not used for orientation, perhaps Allen purposefully omitted them in his discussion. Nevertheless, Allen was certainly aware that Griffin was working on the problem around the time his book would have gone to press, and so it seems a curious omission, even if the results were negative.

perception such as vision. This is much different from what we understand echolocation to be today.

The fact that obstacle avoidance was considered to be simple and mechanistic facilitated the development of technological analogs with these biological phenomena. When Allen considered the unknown function of small "wattles" on the faces of some bats, for example, he suggested that they might "act as receptors for air vibrations set up by passing insects or reflected from near-by objects."[51] He grounded this speculation in Sir Hiram Maxim's 1912 proposal of a nautical technology that could detect obstacles in a ship's path by sending out low-frequency tones and recording their echoes via "delicate membranes on board."[52] In fact, when Maxim first proposed this crude form of sonar in the wake of the *HMS Titanic* disaster (1912), he explicitly pointed to the role played by these membranes in the supposed "sixth sense" of bats.[53] For Maxim, bats offered a biological solution to a technological problem. Although he did not cite Hahn's 1907-08 work, Maxim was probably drawing from it when he explained that bats possessed a sixth sense that detected the reflections of atmospheric vibrations, or "extremely low notes" produced by their flapping wings.[54] Like Hahn, Maxim did not think that bats *heard* the notes, in the traditional sense, for they were thought to be below the threshold of hearing. Instead, he thought the bats' inner ear organs perceived and analyzed the

---

[51] Glover Allen, *Bats*, p. 135.
[52] Glover Allen, *Bats*, p. 137. Allen also briefly noted the conceptual similarity between Maxim's device and other depth-sounding technologies that had been more recently developed to probe the ocean floor. Interestingly, Allen noted the functional similarities between Maxim's proposed technology and the bat "wattles," but he did not point out its similarities to the auditory basis of obstacle avoidance.
[53] Hiram Maxim, "The Sixth Sense of the Bat: Sir Hiram Maxim's Contention. The Possible Prevention of Sea Collisions," *Scientific American Supplement*, Vol. 74 (Sep. 7, 1912): 148-150.
[54] Hiram Maxim, "The Sixth Sense of the Bat," p. 148. In fact, Hahn meant something slightly different by "sixth sense," which for him meant a sense of direction that was based on associative memories whose construction was aided by the sensory organs of the internal ear. It is possible that Maxim was unaware of Hahn's work entirely, in which case he probably had Spallanzani's much earlier explanation of the "sixth sense" of bats in mind.

reflected vibrations "exactly as light waves would be by our eyes under similar conditions." It was thus a certainty, Maxim concluded, that "the bat obtains its knowledge of surrounding objects by sending out certain atmospheric vibrations and receiving back, in a fraction of a second later, the reflected and modified vibrations."[55] In this basic sensory function, Maxim saw the potential for a useful technology—an onboard collision warning system for ships at sea. He proposed a system with three components: a siren driven by a steam-powered electric motor to produce notes of a long wavelength; an "artificial ear" consisting of a drum-shaped cylinder that vibrates and rings a bell in the presence of certain wavelengths; and a similar cylindrical device connected to a mechanism that draws a diagram indicating the amplitude of the reflected wavelengths, providing information about the distance and size of the detected objects.[56]

Maxim and Allen were not alone in recognizing the technological implications of obstacle avoidance in bats. Although he did not cite it in his text, Allen's analysis of obstacle avoidance was probably informed by the more recent work of British sensory physiologist Hamilton Hartridge. In 1920 Hartridge was the first to propose that bats avoided collisions by virtue of emitting high-frequency sounds that reflected off objects in their vicinities, providing the bat with "information concerning its surroundings."[57] In his analysis, Hartridge also likened obstacle avoidance in bats to a technological analog.

Like Hahn, Hartridge devised a series of experiments that allowed him to gauge the ability of bats to avoid obstacles in different sensory conditions. Cruder in their

---

[55] Hiram Maxim, "The Sixth Sense of the Bat," p. 148.
[56] Interestingly, Maxim did not know that the siren had an analog in bat physiology, because he did not think that bats actively produced the sounds whose reflections they perceived. Rather, he thought that they perceived echoes of incidental sounds produced by their wings—mere byproducts of flight. As Griffin and Galambos would later discover, bats in fact emit ultrasonic sounds for the purpose of orientation, functioning analogously to the siren in Maxim's early version of sonar.
[57] Hamilton Hartridge, "The Avoidance of Objects by Bats in their Flight," *Journal of Physiology*, Vol. 54, No. 1-2 (Aug. 1920): 54-57.

design than Hahn's experiments, Hartridge's analysis also lacked Hahn's quantitative rigor. In fact, it seems likely that he was wholly unaware of Hahn's work. Hartridge chose a natural setting for his experimental setup, taking advantage of a building near Cambridge University where a few hundred bats roosted during the summers. Each evening, the bats—he was unsure of the species—were forced to pass between two rooms as they exited the building to hunt insects. Hartridge installed thick shutters and curtains to ensure that these rooms were completely dark. As the bats passed in large numbers through a doorway from one room to the next, he observed that their flight was unaffected by switching on electric lights, which brightened the rooms. Lighting the room left the bats "quite unconcerned," and they continued their swift flight just as they had in the dark. Next, Hartridge manipulated the passageway between the two rooms by gradually closing the intervening door. In both light and dark conditions, he observed that the bats were adept at passing through the opening, but when the gap was reduced to six inches, they passed through only after some hesitation and fluttering. When it was further reduced to four inches, the bats would "as it were come up and look and then fly off without attempting to pass."[58]

Hartridge next strung a series of threads across the room, all of which terminated through a tiny hole inside a cardboard box on the floor. The threads had small weights attached to their ends, and from inside the cardboard box Hartridge used a flashlight to carefully observe the weights, which were designed to bob up and down if a bat collided with a thread.[59] In both light and dark conditions, the bats never struck threads. He therefore concluded that "bats in full flight and in what appeared to be absolute darkness

[58] Hamilton Hartridge, "The Avoidance of Objects by Bats," p. 54-55.
[59] Hartridge did this from within the cardboard box, obviously, to prevent his flashlight from adding light to the room.

can not only steer round a room and avoid one another, but that they can also avoid obstacles such as threads."[60] He dismissed Cuvier's tactile hypothesis straight away, explaining that it seemed "impossible that a bat should be able to fly at an object until it touched it and to then avoid hitting it." Presumably, Hartridge explained, the sense involved in obstacle avoidance should be able to detect obstacles that were still "a considerable distance away." If vision and touch were not involved, did bats possess "some sixth sense not found in the case of man?"[61]

Hartridge was unwilling to accept the existence of a sixth sense until further tests were performed on the ability of bats to detect obstacles using hearing. He cited the work of British naturalist Arthur Whitaker, who in 1906 had found in accordance with Spallanzani's experiments that blinded bats avoid obstacles successfully, but did so poorly when their ear canals were blocked.[62] Although Whitaker noted that the bat's sense of hearing was greatly adapted to "sounds of a much higher pitch than our own," he concluded that hearing was not responsible for obstacle avoidance.[63]

Hartridge, however, did think that Whitaker's observations concerning the bat's sensitivity to high-pitch sound were key to solving the problem. Although he did not perform any experiments demonstrating that bats used their highly developed sense of hearing to avoid obstacles, Hartridge explained the biophysical principles that he believed made it both possible and likely that they did. Sounds of very short wavelength (high-frequency), he explained, were capable of being reflected off objects with a high degree of fidelity (undergoing minimal diffraction). Furthermore, when these sounds struck

---

[60] Hamilton Hartridge, "The Avoidance of Objects by Bats," p. 56.
[61] Hamilton Hartridge, "The Avoidance of Objects by Bats," p. 56.
[62] Arthur Whitaker, "The Development of the Senses in Bats," *The Naturalist* (May 1906): 145-151.
[63] Arthur Whitaker, "The Development of the Senses in Bats," p. 147.

objects, they cast “sound shadows” analogous to those produced by visible light. He therefore put forth an acoustic hypothesis of obstacle avoidance: “I suggest then that bats during flight emit a short wave-length note and that this sound is reflected from objects in the vicinity. The reflected sound gives the bat information concerning its surroundings […] If there are obstacles then these will reflect the sound and the bat will receive an audible warning.”[64]

While he lacked experimental evidence to support this claim, Hartridge did have evidence of a technological analog that was based on the same physical principles. Developed during the First World War, “sound ranging” devices perfected by the British military had “shown that the sense of direction in man can be made use of for estimating the position in space of objects emitting sound waves.”[65] During the war, these devices served to augment the human senses, allowing soldiers to locate and determine the precise distance of enemy weapons based on the acoustic properties of gunshots.[66] Sound ranging involved an array of microphones attuned to the frequency spectrum of gunshots, whose locations could be triangulated by analyzing the differences in time that it took the sound to hit multiple microphones within the array. While sound ranging required large distances between the array itself and the guns in order to generate useful readings, Hartridge explained that if bats emitted sounds of a sufficiently higher frequency than

[64] Hamilton Hartridge, “The Avoidance of Objects by Bats,” p. 56.

[65] Hamilton Hartridge, “The Avoidance of Objects by Bats,” p. 56. Hartridge served in the Royal Naval Air Service at the Kingsnorth experimental station during the war—he most likely learned about sound ranging there. The sense of direction, in this meaning, is taken to indicate the ability of people to localize audibly the source of sounds.

[66] American physicist Robert Millikan observed in 1919 that the most significant scientific problems in war involve communication and navigation in unfamiliar territory, and thus a large share of wartime research focuses on developing technological solutions to these problems. As the history of research on bat orientation shows, animals experience similar problems of navigation, and have evolved physiological solutions that are analogous to these human technologies. Robert A. Millikan, “The New Opportunity in Science,” *Science*, Vol. 50, No. 1291 (Sep. 1919): 285-297. On British sound ranging in World War I, see: W.L. Bragg, “Personal Reminiscences,” in *Fifty Years of X-Ray Diffraction*, ed. P.P. Ewald, p. 533-536 (Utrecht: N. V. A. Oosthoek, 1962).

gunshots, it was physically possible for them to sense objects at much shorter distances. Likening obstacle avoidance to this military technology, he concluded that “it is highly probable therefore that if a bat made use of short wave-length sound it would be able to estimate the position in space of an object ahead of it with considerable accuracy.”[67] In fact, he suggested, this specialized sense of hearing might be capable of forming “sound pictures.”[68] However, Hartridge had no evidence that bats produced sounds with frequencies at or higher than the upper threshold of human hearing.

The Ultrasonic Method of Obstacle Avoidance: A Collaborative Discovery

When Donald Griffin turned his attention in 1938 to the problem of obstacle avoidance in bats, he focused on the work of Hahn and Hartridge. It is unclear whether he knew about Maxim’s crude form of bat-based sonar, although it is possible that Glover Allen had made him aware of it by that point. Nevertheless, despite Hartridge’s intriguing use of the term “sound pictures,” the ability of bats to orient themselves while flying blind was still filtered through the simpler framework of obstacle avoidance. Rather than a general mode of perception such as vision, obstacle avoidance was still assumed to be the result of a simple physiological feedback system, wherein an auditory stimulus elicited an automatically triggered behavioral response. In other words, it was a collision avoidance mechanism.

It was with this mechanistic framework that Griffin approached the distinguished professor of physics George Washington Pierce (1872-1956) in the winter of 1937-38. The director of Harvard’s Cruft Laboratory of Physics since 1914, he had for much of his

[67] Hamilton Hartridge, “The Avoidance of Objects by Bats,” p. 56.
[68] Hamilton Hartridge, “The Avoidance of Objects by Bats,” p. 56.

career been interested in ultrasonic sound and the propagation of electromagnetic radiation.[69] Beginning in July of 1917—just after the U.S. entered World War I—Pierce was among several American physicists and engineers called to work at the Naval Experimental Station in New London, Connecticut. Prompted by the success of German submarine strikes on the Allies, they were tasked with developing technologies that could detect the underwater sound generated by U-boats. Pierce's research group focused on perfecting underwater receivers—"hydrophones"—which were attached to the hulls of ships in order to locate the sources of underwater sound generated by submarines.[70]

Evidently Pierce made a name for himself as a scientific asset for the military: between the first and second world wars, the Navy annually sent him a group of officers eager to learn from an expert about the principles of underwater sound signaling and electrical communication.[71] One of Pierce's longtime friends and fishing buddies, physicist Harvey C. Hayes, also worked on the problem of submarine detection during the First World War. Interestingly, Hayes was partially responsible for achieving Hiram Maxim's earlier vision of an onboard collision avoidance technology, since the submarine detection devices that he helped to develop during the war were also capable of detecting icebergs and other large obstacles via sonic echoes.[72] A physicist at the Naval Research Laboratory, in the 1920s-30s Hayes was a central figure in the

---

[69] Frederick A. Saunders and Frederick V. Hunt, "[Biographical Memoir of] George Washington Pierce," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 33 (1959): 351-380. Pierce was also interested in the propagation of radio waves, and taught courses on the principles of wireless telegraphy.

[70] Hydrophones were placed on both the bows and sterns of ships in order to locate more precisely the sources of the sounds that they received. The physical principle is similar to binaural hearing in vertebrates, with an ear on each side of the head in order to localize sound sources.

[71] Frederick A. Saunders and Frederick V. Hunt, "[Biographical Memoir of] George Washington Pierce," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 33 (1959): 351-380.

[72] See: Harvey C. Hayes, "Detection of Submarines," *Proceedings of the American Philosophical Society*, Vol. 59, No. 1 (1920): 1-47; Harvey C. Hayes, "U.S. Navy MV Type of Hydrophone as an Aid and Safeguard to Navigation," *Proceedings of the American Philosophical Society*, Vol. 59, No. 5 (1920): 371-404.

development of "underwater echo ranging"—what came to be called sonar during World War Two.[73] As the head of the Sound Division at the Naval Research Laboratory, on May 6, 1936, Hayes was also one of a handful of witnesses to the first successful demonstrations of radar at the Naval Research Laboratory.[74] Hayes and his good friend Pierce undoubtedly had much to discuss on their fishing trips.

Back in Pierce's office in January of 1938, Griffin and Pierce pointed the parabolic receiving cone of Pierce's ultrasonic detector at a cage full of bats. They instantly heard a barrage of buzzing and clicking as the instrument translated ultrasonic into audible sound.[75] The highly sensitive device necessitated that Griffin take special care to ensure that the sounds it received were in fact produced by the bats' vocal cords and not by other sources, such as their claws scratching the metallic cage. To eliminate this variable, Griffin gently cradled the bats in his hands while Pierce aimed and monitored the device. After meticulous testing, Griffin and Pierce had obtained unassailable proof that bats indeed produced ultrasonic sounds. The precise physical nature of these sounds (duration, frequency, modulation), however, in addition to their exact function, remained uncertain.

In March of 1938, Griffin and Pierce performed some additional experiments in the Cruft physics laboratory at Harvard. They were joined by James Fisk, a Harvard Junior Fellow and physicist who would in a few short months begin a distinguished career in radar research at Bell Laboratories, where he eventually served as President

[73] Frederick A. Saunders and Frederick V. Hunt, "[Biographical Memoir of] George Washington Pierce," p. 362.
[74] David K. Allison, "New Eye for the Navy: The Origin of Radar at the Naval Research Laboratory," NRL Report 8466 (USGPO: 1981), p. 94-95.
[75] G.W. Pierce and Donald Griffin. "Experimental Determination of Supersonic Notes Emitted by Bats," *Journal of Mammalogy*, Vol. 19, No. 4 (Nov. 1938): 454-455.

from 1959 to 1973. Despite several attempts, Griffin, Pierce, and Fisk were only occasionally able to detect the emission of ultrasonic notes while the bats were in flight. Instead their experiments showed that the bats typically emitted these cries while crawling and just as they took flight. Once in mid-flight, however, the noises apparently ceased. Furthermore, Griffin and Pierce were unable to determine conclusively that bats actually heard the sounds that they produced. They were therefore "appropriately cautious about concluding that these sounds were used for orientation," and instead suggested that the bats more likely produced the sounds as a call or alarm signal.[76]

By the fall of 1938 Griffin and Pierce had concluded that the ultrasonic notes of bats were not used for obstacle avoidance, and so Griffin turned his attention to the equally vexing problem of bird navigation. A few months later, however, he learned that fellow graduate student Robert Galambos was working on a recently developed electrophysiological method to study hearing in mammals. Beginning in the spring of 1939, Griffin and Galambos—"far more of a physiologist" than Griffin—began collaborating on the ultrasonic perception in bats.[77] They eventually demonstrated conclusively that bats avoided obstacles by hearing the reflections of their high-frequency vocalizations—a mode of perception that Griffin would later term "echolocation." With these experiments, Spallanzani's "bat problem" was resolved according to the physiological standards of the day.

---

[76] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 74. In another recollection Griffin referred to their conclusions as "absurdly cautious": Donald Griffin, "Early History of Research on Echolocation," in *Animal Sonar Systems*, ed. Rene-Guy Busnel and J.F. Fish, p. 1-8 (New York: Plenum Press, 1980), p. 2. Interestingly, when Pierce and Griffin published their findings in the fall of 1938 they cited Hahn, but not Hartridge. They certainly had Hartridge's work in mind, though, and did not cite him probably because they cautiously concluded that bats did not use ultrasonic notes for orientation. Apparently because these results were negative with respect to Hartridge's hypothesis, they did not cite it.
[77] Donald Griffin, "Recollections of an Experimental Naturalist," p. 131.

Griffin's uncle Alfred Redfield oversaw Galambos's doctoral research, which was conducted with professor of physiology Hallowell Davis at the Harvard Medical School. Based on the pioneering electrophysiological work of physiologist Alexander Forbes, Davis had become an expert on the subject of "cochlear potentials." In 1927 Forbes had found that when sound strikes the inner ear, an electrical or "cochlear potential" is generated, indicating that the organ is adapted to perceive sound of that frequency.[78] Galambos's research was on guinea pigs, but when Griffin came to him inquiring about the possibility of studying cochlear potentials in bats, he jumped at the chance. Within a few weeks Galambos had shown that bats could indeed detect ultrasonic sound in the same frequency range as their cries.[79]

Even more exciting was their subsequent discovery through careful testing that bats indeed produced ultrasonic sound almost continuously while flying, thus lending credence to Hartridge's auditory theory of obstacle avoidance. Pierce and Griffin had failed to detect this before because they had not realized that the bat's ultrasonic emission was highly directional, and could therefore only be detected if the parabolic receiver was pointed directly in the plane of the bat's forward facing mouth. Thus in the spring of 1939 Griffin and Galambos commenced what would eventually total about three years of collaborative research on obstacle avoidance in bats. Although they decided from the beginning that their work would be the subject of Galambos's doctoral thesis, Griffin's interest in obstacle avoidance was reinvigorated by the discovery of cochlear potentials.

[78] At the time it was understood that cochlear potentials did not necessarily indicate hearing as such, but that they were strongly suggestive of it, and a necessary component of the sensory mechanism. Hallowell Davis et al, "Further Analysis of Cochlear Activity and Auditory Action Currents: With Demonstration of Audible Response," *Transactions of the American Otological Society*, Vol. 23 (1933): 196-216.

[79] Galambos has provided a helpful summary of these experiments, including records from his lab notebook. Robert Galambos, "The 1939-40 Bat Experiments that Validated Jurine's Claim," *Le Rhinolophe*, Vol. 11 (1995): 17-25. The title specifies Jurine (Switzerland) instead of Spallanzani (Italy), because the article was produced at the request of a Swiss journal.

A few months later during the summer of 1939, Griffin was a research fellow at the Huyck Preserve in Rensselaerville, New York, where he continued his own doctoral work on the problem of bird navigation. The question of bat orientation still weighed heavily on his mind, though. After he finished several bird navigation experiments at the beginning of the summer, he decided to spend the remainder of his fellowship banding bats and repeating Hahn's 1907 obstacle avoidance experiments for himself. With the recently acquired knowledge that bats produced and heard ultrasonic sounds while flying, perhaps he would notice something that Hahn had missed. Akin to his research on birds, these experiments were designed to isolate specific sensory capabilities in order to test their effects on obstacle avoidance.

At the Huyck Preserve, Griffin adapted a small horse-stall—nine feet square and seven feet tall—to perform some preliminary experiments. For these tests, he captured twenty-eight bats in total (mostly *Myotis lucifugus*—little brown bats), testing each on the same day it was captured or the following day. Like Hahn, he divided the room in half using an array of metal wires, one millimeter in diameter. Whereas Hahn's wires were unevenly spaced, Griffin suspended them from the ceiling at intervals of thirty centimeters—just large enough for the bats to pass through with their wings fully spread. He also only counted "trials" when bats crossed from one side of the room to the other—if a bat approached the wire and turned back, or if it struck a wire but did not cross to the other side of the room, he did not include the result. He reasoned that only counting trials in which the bats crossed the room would yield data that were more comparable given the different experimental conditions. "Hits" were easily detectable by the vibration of the taught wires and the sound they produced when struck by a bat. A low percentage of hits thus constituted "good avoidance, and a high score [indicated] little or no ability to dodge the wires."[80] No bats were able to dodge the wires perfectly, but a comparison of normal, blinded, and deafened bats nevertheless confirmed that obstacle avoidance depended on the sense of hearing.

It was important to Griffin that the sensory impairments he employed were reversible, unlike those of his predecessors. For example, to blind his bats Spallazani had surgically excised their eyeballs, slicing their optic nerves in the process. Griffin, however, applied a "dark blue collodion mimeograph correction fluid" that dried in a few minutes, rendering the bats completely (but only temporarily) blind. After the tests were performed, it was easily removed with a solution of ether. This was not only more palatable to Griffin, who cared for the animals and did not wish to do them harm, but it had experimental value. Reversible impairments meant that obstacle avoidance could be measured in normal conditions both before and after the experimental conditions, thus yielding data that could account for the possible fatigue that bats experienced while undergoing numerous trials. To deafen his bats, Griffin cleverly inserted small glass tubes into their ear canals and plugged them with thread dipped in collodion fluid. This decision too had a certain logic. By removing the threaded plugs, the bat's hearing was restored, but the potentially uncomfortable tubes remained in place. Thus Griffin could account for the possible effect that the discomfort had on the bat's ability to avoid obstacles. After this, the tubes were removed, restoring the bat to its earlier condition.

Back at Harvard between September of 1939 and the spring of 1940, Galambos joined Griffin in laboriously extending the experiments in a more controlled

---

[80] Donald Griffin and Robert Galambos, "The Sensory Basis of Obstacle Avoidance in Bats," *The Journal of Experimental Zoology*, Vol. 86, No. 3 (Apr. 1941): 481-506.

environment—a 180-square-foot soundproof chamber in the Cruft Laboratory.[81] Including Griffin's experiments at the Huyck Preserve, in total they tested the obstacle avoidance of 144 bats in normal conditions, and 48 under various experimental sensory conditions. While these experiments were generally similar to Hahn's, Griffin and Galambos introduced modifications with the express intention of testing an ultrasonic hypothesis of obstacle avoidance. For example, during the sensory impairment trials they used Pierce's parabolic receiver to monitor carefully the bats' emission of supersonic sounds as they approached the wires. Additionally, Harold E. Edgerton, a photographic engineer from the Massachusetts Institute of Technology, took high-speed pictures of bats as they passed through the wire barricade, allowing Griffin and Galambos to study how the bats maneuvered their bodies in flight while avoiding the wires. They also tested obstacle avoidance in bats whose mouths were tied shut, thus rendered incapable of emitting sound. The results of their experiments were published in the spring of 1941. About a year later, they published a comprehensive analysis of bats' ultrasonic cries, followed by Galambos's paper on cochlear potentials in bats.[82] Together, these three papers represent the published core of their discovery.

In total, they tested obstacle avoidance under normal conditions (no sensory impairments) in 144 bats. The Huyck Preserve experiments were performed during the summer, and thus Griffin was able to use bats caught in their nearby roosts. For the experiments in the fall, however, he had to catch bats hibernating in their New England

[81] They published their results in early 1941. Donald Griffin and Robert Galambos, "The Sensory Basis of Obstacle Avoidance in Bats," *The Journal of Experimental Zoology*, Vol. 86, No. 3 (Apr. 1941): 481-506.

[82] Robert Galambos and Donald Griffin, "Obstacle Avoidance by Flying Bats: The Cries of Bats," *Journal of Experimental Zoology*, Vol. 89, No. 3 (Apr. 1942): 475-490. The delay in publishing these results gave Galambos more time to work-out the "cochlear microphonics" or ultrasonic reception in bats, and it gave them both more time to experiment with and analyze the physical properties of bat sounds.

caves. These were kept in cold storage until they were needed for experiments, as they awoke a few minutes after being brought to room temperature. Like Hahn, Griffin and Galambos found much variation in the ability of normal bats to avoid collisions, but on average the 144 bats struck wires in 34% of their trials.[83] In order to ensure that their experiments accurately captured the effects of sensory impairments on obstacle avoidance, Griffin and Galambos selected the most successful flyers for use in the experimental groups. "Otherwise a treatment which interfered with the ability might not have been recognized as such because the bat's skill was impaired even in the control series."[84] Hence, bats in the experimental groups but with their senses still intact frequently outperformed the average of normal bats.

Of the 28 blind bats that Griffin and Galambos tested, none showed any difference in its ability to avoid obstacles under normal conditions. Like Hahn, they found that bats curiously performed slightly better when blind—in 3,021 total trials, 28 bats struck wires 30% of the time with their vision intact, versus a hit-rate of 24% in 2,016 trials when blinded. To deafen the bats, Griffin and Galambos employed two methods. As described earlier, one method involved inserting glass tubes into the ear canals. The other entailed tightly filling the ear canals with cotton and folding the outer ear structure (the pinna) over the cotton, sewing its edges together so that the cotton was held firmly in place, totally obstructing the ear canal. Noting that the pinnae contain few blood vessels, Griffin explained that bats "did not even seem to resent this sewing

[83] They tested five species in normal conditions: 129 *Myotis lucifugus* (little brown bat), nine *Myotis septentrionalis* (northern long-eared myotis), one *Myotis sodalis* (indiana bat), one *Pipistrellus subflavus* (eastern pipistrelle), and four *Eptesicus fuscus* (big brown bat).
[84] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 487.

process any more than they resented merely being held in the hand."[85] In all cases the deaf bat's flight "became strikingly abnormal and its ability to avoid obstacles was drastically impaired."[86] The hit-rate of 29 bats in this group increased from 31% under normal conditions to 66% when deafened. Griffin and Galambos used a Fisher chi square to determine the statistical significance of their results, which they found to be greater than 99%.[87] Obstacle avoidance seemed very clearly to depend on hearing.

As Hahn had also found, deafened bats were very reluctant to leave the ground, and so Griffin frequently had to drop them from high in the air in order to coax them into flight. He and Galambos analyzed the nature of collisions using high-speed photography, finding that as the deafened bats approached the wires, as well as the walls, they rarely changed their flight patterns as they did in normal conditions while approaching obstacles. Even after striking a wall, the bats frequently continued their forward flying motion, bumping the wall continuously as they gradually fell to the ground: "it seemed as though the bat continued to fly forward as long as it heard no warning sound reflection even though its nose had already bumped the wall."[88] Bats tested at the Huyck Preserve did not show this same tendency, a phenomenon Griffin explained on the physical properties of sound absorption. The wooden walls of the horse-stall, he thought, "reflected enough of the sound emitted by the bat to penetrate the less efficient ear plugs used in those earlier experiments."[89] Using better ear plugs and mostly soundproof walls, the experiments at the Cruft Laboratory yielded deafened bats that were even more helpless.

[85] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 494.
[86] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 489-491.
[87] The test was named for its inventor, British mathematician and population geneticist Ronald A. Fisher.
[88] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 492.
[89] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 492.

Griffin's and Galambos's experiments also entailed a few extra controls that Hahn had not used, since their working hypothesis was Hartridge's auditory theory and they specifically wanted to isolate the role of hearing as accurately as possible. For example, because blind bats flew slightly better than normal bats, they also blinded bats that were already deafened, finding that it had no effect on obstacle avoidance. They also tested bats with glass tubes in their ears, but unplugged by thread so that their hearing remained normal. Despite any degree of discomfort generated by the presence of the tubes in the inner ear, they did not significantly impair obstacle avoidance, just as Griffin and Galambos expected. Bats with only one ear impaired were also tested, and they found that these bats struck obstacles almost as frequently as they did when completely deaf. These "one ear" bats, however, did not bump into walls as they had when completely deafened, indicating that perhaps "one ear is sufficient to inform the animals of the general proximity of a large obstacle."[90] Interestingly, this evidence seemed to contradict the accepted biophysical explanation of sound localization—namely, that localization depended on differences in phase and intensity between two ears, separated in space. Griffin and Galambos explained that "the chief difference between 'one ear' bats and deaf ones is that the former turn away from obstacles and land normally on walls. These bats may be warned of the obstacle simply by the fact that the reflected sound, although heard with only one ear, nevertheless becomes louder as the bat flies forwards."[91]

Galambos had the brilliant idea to also test bats that were prevented from emitting sounds. According to their hypothesis, this should impair obstacle avoidance in the "gagged" bats in much the same way as in deaf bats. They gagged the bats by tying

[90] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 496.
[91] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 497.

thread around the snouts and sealing the lips shut with collodion, taking care to leave the nostrils open for breathing. Griffin and Galambos pointed the ultrasonic detector at the gagged bats as they flew in order to confirm that the seal was tight. "Gagged bats flew in the same clumsy, hesitant, and bewildered manner as deaf bats."[92] The hit-rate of six bats increased from 38% to 65% when they were gagged. This increase was "just as serious as that which results from covering the ears," and similarly yielded a 99% probability of statistical significance.[93]

Like Hahn, they also calculated the probability that objects roughly the size of bats would collide with wires if randomly projected across the room. This analysis was aided by Edgerton's high-speed photography, which made it possible for Griffin and Galambos to determine the variable and average wingspans of bats as they flew between the wires. Using some fairly complex mathematics, they determined that bats should strike wires in 76% of trials if they were totally unaware of them. Using cues besides reflected sound, bats could reduce their hit-rates only to 65%: "this evidence supports the hypothesis that other senses than hearing play a very minor role, if any, in obstacle avoidance by flying bats."[94]

Griffin and Galambos also conducted a few smaller-scale tests to further eliminate non-auditory explanations. One such test evaluated the tactile theory of obstacle avoidance via membranes in the wing, even though they accepted that Hahn had conclusively invalidated Cuvier's long-accepted hypothesis. They covered one bat's wings with collodion, comparing its obstacle avoidance in both normal and deaf conditions, finding that it made no difference. Another test was designed to determine

[92] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 498.
[93] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 499.
[94] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 504.

what role, if any, was played by spatial memory. Griffin assumed that "bats might have a well-developed sense of the direction of their motion and acceleration, arising from [the inner-ear labyrinth]. They could then fly by a sort of dead reckoning when thoroughly familiar with a cave, making certain turns at definite intervals which they remember from countless previous flights."[95] The bats they tested, however, showed no signs of "learning" the layout of the room. In fact, a few of the experiments employed bats that were already blind when first released into the room, and they performed similarly to normal and blind bats that had first encountered the room with their senses intact. This made it "obvious that dead reckoning by means of labyrinth memory could not account in any important degree for the flying skill of sightless bats."[96]

It seems curious that Griffin and Galambos did not perform these tests as rigorously as they did, for example, those with deaf and blind bats. In fact the chi square could not even be used since they performed so few trials. This can be explained by the fact that their tests were designed with a specific working hypothesis in mind, and thus it was most important for them to demonstrate that deafened and gagged bats had significant difficulties avoiding obstacles. Other experiments, like those on spatial memory that were described qualitatively, seemed to anticipate possible objections to their conclusions, and thus functioned more as additional controls that demanded less serious consideration.

Nevertheless, Griffin and Galambos were confident that their results confirmed via inferential reasoning the validity of Hartridge's auditory theory, with a few modifications. Flying bats avoided obstacles by emitting ultrasonic notes that reflected

---

[95] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 501. Griffin was familiar with this so-called "kinesthetic" sense from his concurrent work on bird navigation.
[96] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 501.

off obstacles and were heard by bats. The reflected sound was localized "binaurally by some auditory mechanism, similar in principle to that used by other mammals for sounds of ordinary frequencies."[97] While these experiments seemed to represent the final act in a 150-year drama that opened with Spallanzani alone onstage, Griffin and Galambos saw the need for two more scenes.

The first of these final components, although it was in fact published second, was Galambos's doctoral work on the auditory physiology of bats.[98] Between 1939 and 1941, Galambos showed that supersonic sounds elicited cochlear potentials in bats. That alone was not enough to prove that bats actually heard the sounds, though. According to the physiological standards of the day, proof of hearing required that Galambos show that cochlear potentials stimulated the contraction of the intra-aural muscles, which in turn vibrated the bones of the inner-ear. Over the course of several months, Galambos was eventually able to show that according to this physiological definition of hearing, bats indeed responded to ultrasonic sounds up to at least 55,000 cycles per second (55 kHz).

Of more importance was the analysis of the cries of bats. If bats used supersonic sounds in the manner claimed, Griffin and Galambos reasoned that they ought to show firm evidence that bats indeed emitted them for the purpose of obstacle avoidance during flight. They should also analyze the nature of these sounds, so as to acquire a better understanding of how bats actually utilized echoes to avoid obstacles. They wanted to show, for example, whether the frequency of ultrasonic sounds varied in the detection of

[97] Griffin and Galambos, "The Sensory Basis of Obstacle Avoidance," p. 505.
[98] The portion of his thesis on cochlear potentials was not published until 1942: Robert Galambos, "Cochlear Potentials Elicited from Bats by Supersonic Sounds," *Journal of the Acoustic Society of America*, Vol. 13 (July 1942): 41-49. His these also included a survey of the history of echolocation research, much of which he and Griffin were unaware of by the time they confirmed Hartridge's auditory theory of obstacle avoidance in 1941.

thin wires versus large walls. Furthermore, they wondered if changes in the rate of emission were detectable during obstacle avoidance.

Griffin and Galambos mostly omitted analysis of ultrasonic sound in their 1941 paper on obstacle avoidance. However, while performing these experiments they used Pierce's ultrasonic detector to record the properties of bat sounds made during the trials. They coded the detected sound according to the results of individual trials, recording whether the bat missed the wire, lightly brushed it, struck it while flying through, or hit it directly. This data allowed them to analyze the nature of bat cries that accompanied various levels of success in obstacle avoidance. They found that bats actually produced sounds of three general types: shrill, audible cries analogous to the "vocal cries of other animals"; faint clicks or buzzing sounds while in flight; and a spectrum of ultrasonic sounds produced by bats preparing to take flight and land, and by caged bats "seeking escape."[99] Whereas audible cries were never emitted during flight, the ultrasonic cries were always accompanied by the faint clicks. Like their ability to avoid obstacles in normal conditions, the intensity of ultrasonic cries was highly variable in different species and in individual bats.

Because of their supposed role in obstacle avoidance, analysis of ultrasonic notes was crucial. Griffin and Galambos found that bat sounds were emitted in "short bursts" lasting no more than two-hundredths of a second. The rate of ultrasonic bursts, however, could vary from as few as five per second to as many as sixty, depending on

[99] Robert Galambos and Donald Griffin, "The Cries of Bats," p. 476-477. A few years later Sven Dijkgraaf, a Dutch physiologist, independently confirmed Hartridge's hypothesis. Instead of ultrasonic sound, however, he initially proposed that bats heard the echoes of the faint, audible clicks.

circumstances.[100] While the loudness, frequency, and duration of ultrasonic bursts apparently remained constant while in flight, the "number of cries emitted each second […] depends on where the bat is and what it is doing."[101] While resting, bats emitted bursts at a rate of about five to ten per second. When they began to fly, however, this increased to twenty or thirty per second. Moreover, obstacle avoidance data from several trials of blind bats showed that as the bats approached the wires, their emission rates increased from about 30 to 50 bursts per second. Just as the bats were successfully passing through the wires, their ultrasonics dropped back down to 30 per second—the average rate of bats flying in "unobstructed space."[102] As Griffin and Galambos explained, this transition "was abrupt and unmistakable in 87% of the recorded misses."[103] Bats that did collide with the wires, however, only changed their ultrasonic emission rates 20% of the time. Deafened bats maintained constant emission rates in nearly all of the trials, regardless of whether or not they struck or missed the wires. Thus the emission rates "seem to be correlated with the position of the bat with respect to obstacles."[104]

Once again, Griffin and Galambos concluded that these facts strongly indicated that obstacle avoidance was an "auditory phenomenon" and that the ultrasonic sounds emitted by bats were "essential for normal obstacle avoidance."[105] Having provided evidence that bats produced and heard ultrasonic sounds, and that the ability to produce

---

[100] In their article, Galambos and Griffin explained that they had yet to find the "physiological mechanism"—mechanical or muscular—that made possible the "extraordinarily high rate of emission of the supersonic cries." Robert Galambos and Donald Griffin, "The Cries of Bats," p. 487.
[101] Robert Galambos and Donald Griffin, "The Cries of Bats," p. 481.
[102] Robert Galambos and Donald Griffin, "The Cries of Bats," p. 481-482.
[103] Robert Galambos and Donald Griffin, "The Cries of Bats," p. 482.
[104] Robert Galambos and Donald Griffin, "The Cries of Bats," p. 487.
[105] Robert Galambos and Donald Griffin, "The Cries of Bats," p. 489-90.

and hear these sounds strongly correlated to their ability to avoid obstacles, Griffin and Galambos felt confident that they had finally resolved "Spallanzani's bat problem."

Conclusion

As Robert Galambos observed decades after these discoveries, he and Griffin were fortunate to be at Harvard in the late-1930s. The discovery that bats produced ultrasonic sounds depended not only on the existence of Pierce's detector, but on the fact that he—a distinguished physicist—kept his door open to a curious biology undergraduate who was acting on a hunch. Similarly, Hallowell Davis was in the department of physiology across the Charles River at the Harvard Medical School. That he was willing to work with Galambos, a biology graduate student, is a testament to both the physiological and interdisciplinary character of Harvard biology in the late-1930s. The particular workshop culture of interdisciplinary science at Harvard in the 1930s and 1940s thus played a crucial role in facilitating this important discovery.[106] As Galambos fondly recalled, "at the moment we were united with our Professors there was only one place in the world where two graduate students could demonstrate that flying bats emit sounds we cannot hear, and that the animals hear and act upon the echoes - and we happened to be there."[107]

But what exactly had Griffin and Galambos discovered? Their obstacle avoidance experiments surely improved upon those of Spallanzani and Hahn, who had already developed the foundation for the auditory hypothesis. Moreover, Griffin and Galambos

[106] Historian Joel Isaac has shown the importance of this brand of interdisciplinarity in the development of the human sciences in the same period. Joel Isaac, *Working Knowledge*: *Making the Human Sciences from Parsons to Kuhn* (Cambridge: Harvard University Press, 2012).
[107] Robert Galambos, "The 1939-40 Bat Experiments that Validated Jurine's Claim," p. 25.

were not even the first to propose the ultrasonic revision of those earlier experiments. By the time Griffin met Galambos, the ultrasonic theory was more than twenty years old, the product of an older British physiologist, Hamilton Hartridge. Although he lacked the experimental evidence that Griffin and Galambos produced, surely scientific priority belonged to Hartridge. Griffin and Pierce certainly deserve credit for first detecting the wide range of ultrasonic sounds that bats produced, but they had initially concluded (erroneously) that these sounds were not used for orientation. Moreover, did Galambos's work on cochlear potentials actually prove that bats could "hear" the sounds they produced? Perhaps physiologically, they did. But "hearing" was a conceptual can-of-worms at the time, as the psychologists and physiologists had their own definitions and standards of evidence for what constituted hearing. Was hearing not by its very nature a subjective phenomenon, especially when considered in animals other than ourselves? Finally, was the sensory phenomenon that they discovered best described by the term "obstacle avoidance"? Did their experiments really show that bats merely used sound to avoid obstacles, or was there something more fundamental lying below the surface?

It is worth noting that in their discussion of bat ultrasonics Galambos and Griffin stated that the "ability to vary the rate of production [of supersonics] is apparently completely under the control of the animal," depending on its location with respect to a detected obstacle.[108] While this might intriguingly appear to be the kernel of a mentalistic explanation of bat orientation behavior, it must be kept in mind that their understanding of obstacle avoidance was entirely mechanistic. Whatever control the bat may have had over its emission was understood as the product of entirely automatic and unconscious physiological mechanisms. The fact that they still thought of these experiments in terms

[108] Robert Galambos and Donald Griffin, "The Cries of Bats," p. 479.

of obstacle avoidance, or as "collision warning system," is a testament to how deeply a mechanistic view of animals was engrained in their thinking.[109] The ability was not thought to be either interactive nor very sophisticated, but instead was thought of as a physiological servo-mechanism, or stimulus response relationship. Griffin and Galambos apparently never considered whether bats might use their sense of hearing to acquire other information about objects within their environments, analogous to how most vertebrates employ vision, for example.

The most important aspect of this discovery did not materialize until December of 1944. It was then that Griffin, heavily engaged in wartime research, published a short article in *Science*, in which he proposed the term "echolocation" to describe the method by which bats orient themselves.[110] In so doing, Griffin subsumed the sensory ability of bats under the same conceptual umbrella as "facial vision" used by blind humans, and more importantly, its technological analogs—radar and sonar used by the military. The fact that radar and sonar were heralded for their role in the struggle to defeat fascism in Europe sanctified these technologies even further in the eyes of technocratic scientists heavily engaged in wartime research. Not only that, linking the organic sensory systems of bats to these military technologies seemingly guaranteed that Griffin's name would be remembered in the history of science at the expense of Lazzaro Spallanzani, Walter Louis Hahn, Hamilton Hartridge, and even Griffin's co-discoverer, Robert Galambos.

[109] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 81.
[110] Donald Griffin, "Echolocation by Blind Men, Bats and Radar," *Science*, Vol. 100, No. 2609 (Dec. 1944): 589-590.

In my next chapter, I explore the contours of this discovery more fully, showing how Griffin's conception of echolocation was shaped by unexpected developments in his wartime research.

CHAPTER 3
The Wartime Discovery of Echolocation

Introduction

This chapter focuses on the transformation of Donald Griffin's understanding of the physiological basis of bat orientation from an obstacle avoidance mechanism to the more general method of echolocation. Over several years following his initial experiments, Griffin came to understand the sensory physiology of bats to entail more than a mere collision warning system based on ultrasonic echoes. In fact, it was three years later in late-1944, well after he ceased doing experimental work on bat orientation, that he coined the term "echolocation." At that time he had been deeply engaged in wartime research for several years, and bats remained firmly on the backburner. Griffin conceptualized echolocation as an active process by which bats acquired information via the perception of echoes generated by their ultrasonic signals. As opposed to obstacle avoidance, understood as a simple and automatic mechanism that served a specific function in flight, echolocation was a general mode of perception that allowed bats to acquire information about the structures of their environments and the objects that they encountered within them. Echolocation was thus more general than its precursor, and it implied that bats actively utilized this physiological tool for a wider range of behaviors and interactions with their environments. In the years following the war, the study of echolocation and its role in the bat's life would gradually yield insights into several new problems. These included echolocation's inherently limited range, difficulties in target discrimination, its use in hunting prey, its susceptibility to jamming by other bats' ultrasonic signals, and even jamming by certain species of moth that bats hunted.

Most scholarship on Griffin erroneously points to his collaboration with Robert Galambos between 1938 and 1940 as the *experimentum crucis* of echolocation's discovery.[1] As important as those experiments were, however, they in fact proved no such thing. Rather, that experimental work showed that bats produced ultrasonic sounds and that they were capable of obstacle avoidance by hearing the echoes of those cues—thus proving Hartridge's auditory hypothesis. Galambos's electrophysiological work on bat cochlear microphonics further demonstrated that bats indeed could perceive sounds in the ultrasonic range. Through those experiments, Griffin and Galambos discovered a mechanistically construed behavior; that is, the bat's ability to avoid obstacles via hearing echoes of sounds they emitted was a simple and automatic sensory function, confined to a specific aspect of flight.

By 1941, Griffin had largely abandoned work on bat orientation, and focused almost exclusively on his doctoral thesis, which concerned the problem of bird navigation—another perplexing topic in the behavioral wheelhouse of sensory physiology. After finishing his thesis in the spring of 1942, he spent several years in various Harvard laboratories working on wartime projects for the military. What prompted Griffin in December 1944, nearly three years after he ceased major experimental work on bats, to publish a brief article in which he insisted that a new concept and term were necessary to describe their mode of physiological perception and orientation? The extant scholarship on Griffin fails to address this important question.

[1] See, for instance: Eileen Crist, "Griffin, Donald Redfield," *Complete Dictionary of Scientific Biography,* Vol. 21 (Detroit: Charles Scribner's Sons, 2008), p. 177-186; Carolyn Ristau, "Donald Redfield Griffin," *Proceedings of the American Philosophical Society* 149 (Sep. 2005): 399-411; Charles Gross, "Donald R. Griffin," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 86 (2005): 1-20; H. Raghuram and G. Marimuthu, "The Discovery of Echolocation," *Resonance*: *Journal of Science Education*, Vol. 10 (Feb. 2005): 20-32. Galambos did not participate in the 1938 experiments on the bat's production of ultrasonic sound, but was Griffin's equal partner in their subsequent work on obstacle avoidance between 1939 and 1941. These experiments are explained in my previous chapter.

Eileen Crist, for example, makes no mention of that wartime work, and refers to Griffin and Galambos as co-discoverers of *echolocation*, citing their 1941 paper on obstacle avoidance.[2] Similarly, Charles Gross points to Griffin's graduate work with Galambos as the key moment in the discovery of echolocation. Gross only briefly alludes to Griffin's wartime experience, and fails to show how it affected his view of echolocation or his broader approach to sensory physiology.[3] Ethologist Carolyn Ristau's important account of her former advisor's life also elides his graduate and wartime work, recognizing Griffin "for that initial discovery of bat echolocation with Robert Galambos (1938) and for subsequent years of study."[4] The conflation of obstacle avoidance with echolocation obscures the significant influence of the wartime context in an important scientific discovery. To explain the nearly three-year gap between Griffin's discovery of obstacle avoidance and his development of the concept of echolocation, we must look at his military research and toward Harvard's wartime research complex more broadly.

Although it was not directly related to the sensory physiology of bats, Griffin's wartime research profoundly shaped how he conceived of bats and their use of echolocation. These projects included research on communications and sound transmission at Harvard's Psycho-Acoustic Laboratory (PAL), where physiologists and psychologists studied problems of language, signal transmission, and information processing, all of which were crucial for enhancing military communications technologies. Griffin also spent part of the war at Harvard's Fatigue Laboratory, where he researched the effects of extreme cold on human physiology. Like his work on

---

[2] Eileen Crist, "Griffin, Donald Redfield," p. 178. Crist makes no mention of Griffin's wartime work or his coining of "echolocation" in 1944. Raghuram and Marimuthu similarly conflate the discovery of obstacle avoidance with echolocation.
[3] Charles Gross, "Donald R. Griffin," p. 3.
[4] Carolyn Ristau, "Donald Redfield Griffin," p. 400.

psychoacoustics, this research also sought technical solutions to problems fundamentally rooted in physiology and its relationship to perception. He concluded his wartime research with work on human vision and infrared technologies to enhance night-vision equipment for the military. But aside from his own research, Griffin's scientific thought was also profoundly shaped by a growing awareness of the significant capabilities of remote sensing technologies such as sonar and radar, which, like obstacle avoidance, were initially developed and deployed for simple tasks such as detecting and avoiding obstacles during marine navigation. In early 1942, the Radio Research Laboratory, whose charge was to develop both offensive and defensive radar countermeasures, moved into Harvard's Biological Laboratories. Elsewhere on campus, F.V. Hunt's Underwater Sound Laboratory furiously worked on developing military applications of sonar technology for navigation and weapons guidance systems. Griffin's personal and professional network included several key figures working in these areas. As excitement about radar and sonar swirled around Harvard's campus, he began to consider the sensory physiology of bats as fundamentally analogous to these increasingly sophisticated military technologies.

Historian Joel Isaac has emphasized the significance of interdisciplinary research within the "Harvard complex" in the development of the human sciences during the 1930s-1950s. He argues that hubs of interdisciplinary exchange such as the Society of Fellows and the Psycho-Acoustic Laboratory led to a reformulation in the way scientific knowledge was understood as the negotiated product of practices, rather than of ideological commitments to objectivity. Although Isaac points to the importance of Harvard's unique workshop culture in the development of the human sciences and hybrid fields such as cybernetics and cognitive linguistics, this collaborative atmosphere also played an important role in the biological sciences.[5] As the case of Griffin shows, scientific problems relating to animal behavior greatly benefited by interdisciplinary exchanges between physicists, biologists, and engineers. Griffin's investigation of bats relied on intellectual and technical contributions from physicist George Washington Pierce, physicist and Society Fellow James Fisk, Harvard medicine's Hallowell Davis, sonar pioneer F.V. Hunt, and many others. This open-door culture, which encouraged interdisciplinary exchange, yielded unique applications of physical and engineering approaches to biological research. And this had a significant effect on Griffin's technical approach to behavioral problems, and to his understanding of echolocation as a physiological analog to the military technologies of remote sensing, sonar and radar.

Once Griffin reimagined bat echolocation as a biophysical manifestation of a more general phenomenon, the conceptual parallels between the biological and the technological spheres generated new questions about the abilities of bats. Rather than being merely a collision warning system—a technology perhaps worthy of admiration in the First World War, but certainly not in light of developments brought on by the technical sophistication of the Second World War—bat echolocation was a complex mode of perception. Like radar operators, bats used echolocation to locate and to discriminate amongst objects of relative importance with great accuracy. Did bats deploy their biological sonar to hunt prey, as naval officers used sonar and Army Air Force pilots

[5] Joel Isaac, *Working Knowledge: Making the Human Sciences from Parsons to Kuhn* (Cambridge: Harvard University Press, 2012), p. 169-171. In addition, as Paul Edwards and Hunter Crowther-Heyck have argued, a new focus on information processing in places such as the Psycho-Acoustic Laboratory led eventually to the rejection of behaviorism: Paul Edwards, *The Closed World: Computers and the Politics of Discourse in Cold War America* (Cambridge: MIT Press, 1988); Hunter Crowther-Heyck, "George A. Miller, Language, and the Computer Metaphor of Mind," *History of Psychology*, Vol. 2, No 1 (1999): 37-64. See also: Jamie Cohen-Cole, "The Politics of Psycholinguistics," *Journal of the History of the Behavioral Sciences*, Vol. 51, No. 1 (2015): 54-77; Jamie Cohen-Cole, *The Open Mind: Cold War Politics and the Sciences* (Chicago: University of Chicago Press, 2014).

used radar? Was echolocation, as its technological cousins, subject to "jamming" by other signals? These questions only became valid once Griffin started thinking about echolocation as a general method that was analogous to these technologies. As he later explained, "echolocation of stationary objects had seemed remarkable enough, but our scientific imaginations had simply failed to consider, even speculatively, this other possibility"—that bats used echolocation to hunt their prey—"with such far-reaching ramifications."[6] Indeed, Griffin's wartime experience at Harvard was crucially important in expanding what he referred to as his "scientific imagination."

Psychoacoustics, Physiology, and Perception: Donald Griffin's Wartime Research

After receiving his doctorate in the spring of 1942, Griffin suspended his Junior Fellowship (Society of Fellows) and spent the war years in several Harvard laboratories, where he pursued a variety of military research projects. His first major stint was in Harvard's Psycho-Acoustic Laboratory (PAL), where he worked on the physiology and psychology of sound transmission and reception for military communications. In late-1942 Griffin left PAL for the Harvard Fatigue Laboratory, where he worked on problems concerning the physiology of soldiers in extreme conditions. After leaving the Fatigue Lab in May of 1944, Griffin worked briefly on human vision and infrared night-vision technology in Harvard's Biological Laboratories. Griffin's applied military projects do not constitute a diversion from a career otherwise dedicated to animal behavior and physiology. Rather, this research shares fundamental connections with his more general scientific interests. Moreover, his work calls attention to some of the understudied

[6] Donald Griffin, "Recollections of an Experimental Naturalist," in *Leaders in the Study of Animal Behavior*, ed. Donald Dewsbury, p. 120-142 (Cranbury, NJ: Associated Universities Press, 1985), p. 138.

activities of wartime biologists and physiologists, whose contributions are often ignored in historical scholarship that focuses on the physical sciences in the service of the state during World War II and the Cold War. His first wartime stint was in Stanley Smith Stevens's Psycho-Acoustic Laboratory, where Griffin found it "exhilarating to plunge directly into practical efforts to improve voice communication systems" for the military.[7]

In 1940 the U.S. Army Air Forces requested through the National Defense Research Committee (NDRC) the establishment of two laboratories, the Psycho-Acoustic Laboratory (PAL) and what would later be called the Electro-Acoustic Laboratory (EAL), whose joint-function was to study among other things, the effects of extreme noise in the modern warfare environment.[8] NDRC leadership chose Harvard University as the institutional sponsor, and psychologist S.S. Stevens, pioneer of psychophysics, was selected to head PAL.[9] In the fall of 1942 the NDRC was reorganized as one of several units under the much larger Office of Scientific Research and Development (OSRD), the result of President Roosevelt's and other military leaders' realization that the war effort would require a much vaster research and development infrastructure in order to coordinate the work of scientists with industry and the military.[10] PAL's administrative and funding structure was thus officially subsumed under Division 17 of the NDRC (now a subunit of OSRD), which was composed of twenty-three divisions, panels, and

---

[7] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 76.

[8] For a brief history of the psychological work at PAL, see Paul Edwards, *The Closed World: Computers and the Politics of Discourse in Cold World America* (Cambridge: Massachusetts Institute of Technology Press, 1997), especially chapter seven; Hunter Crowther-Heyck, "George A. Miller, Language, and the Computer Metaphor of Mind," *History of Psychology*, Vol. 2, No 1 (1999): 37-64.

[9] Psychophysics concerns the relationship between physical stimuli and sensation in the sensory systems of humans and animals. For more on Stanley Smith Stevens, see: George A. Miller, "Stanley Smith Stevens: A Biographical Memoir," *Biographical Memoirs of the National Academy of Sciences of the United States* (Washington DC: National Academies of Science Press, 1975), p. 426-428.

[10] FDR established the OSRD with Executive Order 8807 on May 27, 1941 "for the purpose of assuring adequate provision for research on scientific and medical problems relating to national defense."

committees.[11] Division 17, the "Physics" division, was broadly construed and "fell heir to a myriad of miscellaneous problems of a physical nature which, in themselves, were not often interrelated."[12] Consequently, three subdivisions were created to better coordinate its disparate activities. The "Acoustics" subdivision (17.3), chaired by physicist and sound expert Harvey Fletcher, was established specifically to incorporate ongoing PAL research related to the "shattering noise of modern war," and the vast majority of the subdivision's work was conducted in the two Harvard laboratories in coordination with industrial partners such as Bell Labs.[13] In early 1942 Griffin joined the lab, which quickly expanded to over fifty investigators due to the intensity of wartime research.[14]

PAL's research was reported and internally circulated among scientists, military leadership, and engineers through hundreds of OSRD reports, which summarized various acoustical problems, technical solutions, and recommendations for the development of

---

[11] The NDRC initiated research projects at the request of the Army and Navy, or on behalf of American allies through the OSRD Liaison Office. After its reorganization was finalized in December 1942, the NDRC reviewed the projects proposed by the various divisions and panels, making recommendations to the office of the Director of the OSRD (Vannevar Bush, Director). The NDRC was chaired during the war by James B. Conant, who was supported by Army Representative Roger Adams, Navy Representative Frank B. Jewett, and Commissioner of Patents Karl T. Compton, in addition to several other scientists and military leaders. For a full administrative history of NDRC and OSRD, see especially chapters two through six in: Irving Stewart, *Organizing Scientific Research for War: The Administrative History of the Office of Scientific Research and Development* (Boston: Little, Brown and Company, 1948).

[12] Charles Waring, preface to *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3, ed. Charles Waring (Washington DC: NDRC, 1946), ix. Accessed at the Library of Congress Division of Scientific and Technical Reports. During the war approximately $8.4 million was authorized under Division 17, a relatively modest amount compared to larger divisions such as Division 14 (Radar), which spent about $120 million between January 1943 and June 1946. Physicist Paul E. Klopsteg served as chief of Division 17 until 1945, when MIT physicist George R. Harrison took over in March of that year. Irving Stewart, *Organizing Scientific Research*, p. 92-94.

[13] Charles Waring, preface to *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3, ed. Charles Waring (Washington DC: NDRC, 1946), ix. Accessed at the Library of Congress Division of Scientific and Technical Reports. Fletcher, a renowned expert on sound, was director of physical research at Bell Labs from 1935 until his retirement after the war. Stephen H. Fletcher, "Harvey Fletcher: A Biographical Memoir," *Biographical Memoirs of the National Academy of Sciences of the United States* (Washington DC: National Academies of Science Press, 1992).

[14] Griffin's title was "Special Research Associate."

instrumentation that would facilitate communication in military engagements.[15] As Stevens summarized the work generally, "The problems of reducing noise, protecting personnel, avoiding detection by the enemy or confusing his intelligence are issues that must be faced by a modern armed force […] To this state of affairs, the answer, of course, was research—scientific inquiry into the conditions of use, the causes of failure, the specifications for success."[16] Griffin participated in several projects at PAL and was listed as primary researcher or co-author on three OSRD reports.[17] Analysis of these reports, all declassified in 1960, serves to characterize his wartime work on psychoacoustics.

Circulated in August of 1942, "The Acoustic Design of Earphone Sockets for Helmets and Headsets" was the first published report detailing Griffin's work at PAL.[18] A technical analysis of various designs of earphone cups, the report compared the noise-insulating properties of several U.S., British, and German aircraft helmets. The main problem that Griffin and his colleagues confronted involved the noisy interior of aircrafts. The clamor was so intense that when radio and interphone (plane-to-plane) signals were amplified in order to cut through the ambient noise, the speech was made unintelligible and/or painful to the human ear: "In extremely noisy airplanes there is, figuratively speaking, no room for speech to be inserted between the noise level of the plane and the

---

[15] Several of these reports, representative of the broad-ranging research at PAL, are summarized in the division's summary report: *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3, ed. Charles Waring, (Washington DC: NDRC, 1946). Accessed at the Library of Congress Division of Scientific and Technical Reports.
[16] S.S. Stevens, "Introduction," in *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3, ed. Charles Waring, p. 1-5 (Washington DC: NDRC, 1946), p. 1. Accessed at the Library of Congress Division of Scientific and Technical Reports.
[17] OSRD reports 826, 901, and 1572. Accessed at the Library of Congress Division of Scientific and Technical Reports.
[18] Donald Griffin, John Volkmann, S.J. Goffard, and S.S. Stevens, *OSRD No. 826* ["The Acoustic Design of Earphone Sockets for Helmets and Headsets"], 20 August 1942. Accessed at the Library of Congress, Division of Scientific and Technical Reports.

upper limit that the ear can tolerate."[19] This was a problem of both physiology and psychology: the carrier signal had to be amplified such that it was loud enough to cut through the ambient noise of the aircraft while remaining intelligible to the listener, but not so loud that it caused pain or damage to the ear. The solution was technical, as Griffin and his colleagues determined that it was necessary to reduce the level of ambient noise through effective insulation of the earcup. Rather than attempting to insulate the aircraft itself to external noise, Griffin's team explained that the best designed helmets and earcups, like those possessed by the German Luftwaffe, were better able to improve the acoustic environment for effective wartime communication.[20] Griffin's team employed speech articulation tests to compare various helmet and earcup designs, taking into account not only the acoustic insulating properties of each model, but also factors including the helmet's comfort and size, the variability of human ear anatomy, the volume of air between the earphone and the ear canal, the effect of changes in air pressure at different altitudes, and the adaptability of standard-issue helmets to include the installation of altered earcups. This research led to the development of a new earcup and helmet design, which the report recommended for adoption by the Army Air Forces.

Other research centered more firmly on perception and information processing in human auditory physiology and psychology.[21] In an expansive eighty-page report, Griffin and his colleagues documented "the outcome of an experimental program designed to test and evaluate the instruments of communication employed in the Services, and to develop

---

[19] *OSRD Report 826*, p. 1. Accessed at the Library of Congress Division of Scientific and Technical Reports.

[20] Meanwhile, in Leo Beranek's more physically oriented Electro-Acoustic laboratory, scientists were engaged in acoustic insulation research in order to tackle the problem of noise pollution from the perspective of the aircraft itself.

[21] J.P. Egan, Donald Griffin, Joseph Miller, and Talbot Waterman, *OSRD No. 901* ["The Performance of Communication Equipment in Noise,"], 1 October 1942. Accessed at the Library of Congress, Division of Scientific and Technical Reports.

methods for improving the transmission and reproduction of speech by interphone and radio."[22] Essentially a summary of the major problems of wartime communication, the report detailed the methods of testing word articulation, the long-term effects of wartime acoustics on human physiology, analysis of the general architecture of the communication systems of the Army and Navy, tests of military equipment such as microphones, amplifiers, interphones and earphones, and the factors that introduced interference into these communication systems. The most relevant aspect of the report to Griffin's work is its explication of PAL's speech articulation tests, which entailed research and methods evenly divided between physiology and psychology.

PAL researchers and test subjects participated in thousands of articulation tests conducted in a large sound chamber in the basement of Harvard's Memorial Hall, in which loudspeakers blasted synthetic noises in order to recreate the variable acoustic environments of battlefields and military vehicles. A team of trained announcers, including Griffin (whose initials "DG" appear throughout speech articulation charts), would read carefully designed word-lists in order to gauge the *articulation score*—that is, the percentage of words that subjects heard correctly, given the constraints of the experiments.[23] The announcer's ability to convey messages successfully was also scored, and incidentally Griffin performed below the mean due to the "consistently hoarse quality in his voice."[24]

[22] *OSRD No. 901*, p.1. Accessed at the Library of Congress Division of Scientific and Technical Reports.
[23] The articulation tests involved four types, which consisted of the variations of acoustic environments involved in transmitting communication: noise-to-noise (plane-to-plane); noise-to-quiet (plane-to-ground); quiet-to-noise; and quiet-to-quiet. See *OSRD No. 901*, p. 6-10. Experiments such as these at PAL also led to reforming the familiar phonetic alphabet employed by the military in their internal communications (alpha, bravo, charlie etc.). Their test subjects were composed mainly of the research staff themselves along with conscientious objectors to the war.
[24] *OSRD Report No. 901*, p. 14. Accessed at the Library of Congress Division of Scientific and Technical Reports.

Even though variables not directly related to electrical apparatus (such as the timbre of the announcer's voice) affected the outcomes of the experiments, articulation scores were interpreted as measuring the quality of communication *equipment*. As historian Paul Edwards has emphasized, this tendency to view the human factor as embedded in vast chains of information processing units had important consequences for PAL's psychologists.[25] Edwards argues that PAL's work, especially that of George A. Miller, directly contributed to the eventual cognitive turn away from the behaviorist paradigm in American psychology: "The PAL played a crucial role in the genesis of postwar information processing psychologies," and a significant number of PAL psychologists made their careers in the emerging field of anti-behaviorist, cognitive approaches.[26] Thus in attempting to account for the "human element" amid a vast system of computing and communications electronics, PAL psychologists began to understand the human role as a crucial cog in a vast "information processing" network. PAL director S.S. Stevens observed, "It was quickly recognized that the human factor in communication is crucial. What clues must the human ear have to hear a spoken message, and what is the nature of the human voice itself?"[27] In order to tackle problems related to the human element, approaches in electrical and acoustical engineering needed to be complemented by laboratory investigations of human perception and psycholinguistics: "War noise thus helped to constitute communication as a psychological and a

---

[25] Paul Edwards, *The Closed World: Computers and the Politics of Discourse in Cold World America* (Cambridge: Massachusetts Institute of Technology Press, 1997).
[26] Paul Edwards, *The Closed World*, p. 212. Hunter Crowther-Heyck has also cited the importance of George Miller's wartime work as influencing his cognitive trajectory in postwar psychology: Hunter Crowther-Heyck, "George A. Miller, Language, and the Computer Metaphor of Mind," *History of Psychology*, Vol. 2. (1999): 37-64.
[27] S.S. Stevens, "Introduction," in *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3, ed. Charles Waring, p. 1-5 (Washington DC: NDRC, 1946), p. 1. Accessed at the Library of Congress Division of Scientific and Technical Reports.

psychophysical problem."[28] Physiologists, biologists, and engineers worked seamlessly with PAL's psychologists, thus creating opportunities for scientists such as Griffin to approach problems of perception and information processing from multiple disciplinary perspectives.[29]

PAL's speech articulation tests were designed to account for factors that included the acoustic environments of the sending and receiving parties, electrical components in the instruments, the effects of learning as subjects (and announcers) became more familiar with common words and sentences, linguistic theories of language acquisition and learning, and the effects of fatigue on perception and articulation.[30] As a result of this work, Griffin and his colleagues recommended that a wider frequency range be used in military electronic communication systems, and that measures be taken to increase the ratio of speech to ambient noise. Furthermore, the report led PAL and Bell Labs to co-develop technical solutions in the form of "magnetic and dynamic earphones" that could convey speech effectively at a much higher frequency than existing devices.[31] The tests also led PAL to revise the military vocabulary and phonetic alphabet in order to increase the intelligibility and efficiency of military communications.[32] Thus their solutions were

---

[28] Paul Edwards, *The Closed World*, p. 214.

[29] As a field of study, information theory was still in its infancy. Claude Shannon's seminal article, "A Mathematical Theory of Communication," would not appear until 1948. However, several figures who would later make important contributions to information theory worked alongside Griffin at PAL, including S.S. Stevens, George Miller, and Griffin's friend and colleague, J.C.R. Licklider. Claude Shannon, "A Mathematical Theory of Communication," *The Bell System Technical Journal*, Vol. 27 (1948): 379-423.

[30] *OSRD Report No. 901*, p. 10. Accessed at the Library of Congress Division of Scientific and Technical Reports.

[31] F.M. Wiener and George Miller, "The Interphone," in *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3, ed. Charles Waring, p. 119-141 (Washington DC: NDRC, 1946), p. 136. Accessed at the Library of Congress Division of Scientific and Technical Reports. The Army Air Forces (AAF) later adopted these earphones.

[32] George Miller, "Intelligibility of Speech: Special Vocabularies," in *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3, ed. Charles Waring, p. 81-85 (Washington DC: NDRC, 1946). Accessed at the Library of Congress Division of Scientific and Technical Reports.

as much technical and physiological as they were psychological. As psychologist George A. Miller explained in the *Summary Technical Report* of PAL's wartime research, the aforementioned "improvements in articulation which [resulted] from increased gain and power constitute very real advantages to bomber personnel to whom the interphone represents the key to teamwork necessary for the successful completion of a mission."[33]

Griffin's earlier research on the sensory physiology of bats no doubt contributed to his special interest in the nature of high-frequency sound. Moreover, a self-described "gadget man," he had a facility with manipulating electronic devices and experimental design in order to serve the needs of his research questions.[34] His wartime investigations into the intelligibility of speech—further documented in *OSRD Report 1572* (circulated July 9, 1943)—involved tests designed to detect the "high- and low-frequency cutoffs" of speech in noisy environments. Equipment that raised the low-frequency cutoff or lowered the high-frequency cutoff (which diminished the intelligibility of sound below or above those boundaries, respectively) made speech less intelligible, especially in unfavorable noise conditions. Griffin and his team reported that "the more difficult the conditions the wider should be the band of frequencies," and they subsequently recommended that interphone equipment (including earphones) ought to have a low-frequency cutoff no lower than 4,000 cycles per second.[35] These investigators thus proved through "laborious tests in a variety of noise fields" what years later would seem obvious: that one "really could hear better in noise with a broad-band system."[36]

---

[33] F.M. Wiener and George Miller, "The Interphone," p. 141.
[34] For example, Griffin's research on bat echolocation required a special experimental setup to account for the highly directional nature of the bat's ultrasonic pulses, which are difficult to capture unless the microphone is pointed directly at the bat's mouth as it emits the pulse.
[35] F.M. Wiener and George Miller, "The Interphone," p. 9.
[36] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 76.

Griffin left PAL in December of 1942, and although his time there was relatively brief, his psychoacoustic work forever affected his approach to sensory physiology. Several years later, for example, he came to view bat echolocation as a phenomenon rooted in language and information—that is, he wondered if echolocation was in a fundamental sense the bat's way of communicating with its environment in order to extract information from it. In his 1959 book, *Echoes of Bats and Men*, Griffin devoted a chapter to the "language of echoes," in which he described the role of orientation sound in echolocation as a "most important message carrier."[37] For Griffin, echoes came to be understood as "a special language of their own," and he wondered, "what is it in a bat's tiny brain that permits understanding of this language and unlocks this library of useful information? No one yet knows the answer."[38] Later in his career, he pursued that line of inquiry more vigorously, explaining that "echolocation is essentially a solipsistic form of communication as far as we know. The animal emits an orientation sound, hears the echoes, and alters its behavior in an appropriate fashion based upon the information conveyed by these echoes […] Animals thus endowed might find the analytical requirements of an advanced communication system already at their disposal."[39] The culmination of these ideas would eventually come in the late-1970s, when Griffin described echolocation as a metaphorical form of communication in his analysis of animal consciousness.[40] Although he did not consider this linguistic interpretation of

[37] Donald Griffin, *Echoes of Bats and Men* (Garden City, NY: Anchor Books, 1959), p. 83.
[38] Donald Griffin, *Echoes of Bats and Men*, p. 104-105.
[39] Donald Griffin, "Echolocation and its Relevance to Communication Behavior," in *Animal Communication*, ed. Thomas Sebeok, p. 154-164 (Bloomington: Indiana University Press, 1968), p.154-156.
[40] In my final chapter, I analyze Griffin's work on animal consciousness in greater detail.

echolocation until many years after the war, some crucial seeds were no doubt planted during his time at PAL**.**

In December of 1942, Griffin left PAL and moved to Harvard's Fatigue Laboratory, where he would spend the next eighteen months working on problems ranging from physiological thermodynamics to the bends.[41] The Fatigue Lab, unlike PAL and EAL, was not created specifically to serve the scientific needs of the state.[42] Established in 1927, the lab was a highly interdisciplinary institution that "represented a concept unique in biological research—that the systems and organs which comprise a biological organism are interrelated and need to be studied in that context if its biological and social functioning is to be fully understood."[43] In the twenty years of its existence, psychologists, physiologists, biochemists and other specialists working together at the Fatigue Lab researched a wide range of topics that included metabolism, nutrition, aging, the physiochemical properties of blood, and climatic stress.[44] During the war, one of the lab's major undertakings was to measure the physiological effects of extreme environments on soldiers. Griffin worked there from January 1943 until June 1944, and his research was largely technical in nature. He spent most of his time testing and developing cold weather clothing; this apparently left him somewhat unsatisfied, as he complained to his doctoral advisor Karl Lashley: "There have also been some opportunities for research of a broader interest on high altitude decompression sickness

---

[41] Donald Griffin, S. Robinson, H.S. Belding, R.C. Darling, and E.S. Turrell, "The Effects of Cold and Rate of Ascent on Aero-Embolism," *Aviation Medicine*, Vol. 17 (Feb. 1946): 56-66.
[42] For a general history of the Harvard Fatigue Laboratory, see: Steven M. Horvath and Elizabeth C. Horvath, *The Harvard Fatigue Laboratory: Its History and Contributions* (Englewood Cliffs, NJ: Prentice-Hall, 1973). Chapter seven concerns the lab's wartime work, although Griffin is only mentioned briefly.
[43] Steven Horvath and Elizabeth Horvath, *The Harvard Fatigue Laboratory*, p. 3.
[44] The Fatigue Lab was dissolved due to administrative and funding problems during its transition to peacetime research. For a representative discussion of its scientific contributions, see: Steven Horvath and Elizabeth Horvath, *The Harvard Fatigue Laboratory*, p. 87-180. G. Edgar Folk, who worked at the lab during the war, has also noted that Harvard president James Conant was never a strong supporter of the lab.

and on what I call the 'physiological thermodynamics' of clothing […] However, it is very difficult to put in much time on even as basic questions as these due to the pressure of specific garments to be tried and criticized."[45]

Sources that concern Griffin's work at the Fatigue Lab are scarce, but his longtime colleague, physiologist G. Edgar Folk, documented his experience there, which included a substantial amount of collaborative work with Griffin.[46] In addition, Griffin's archival papers contain an unpublished report summarizing his major lines of research there.[47] In one extended experiment on the effect of cold weather on metabolism, for example, Griffin had Folk remain in the lab's -40˚F cold room for twelve straight hours. In order to gauge the effects of the freezing European winter on the physiology of allied soldiers, Griffin measured Folk's metabolism by recording the amount of oxygen consumed in each inhalation. After establishing the feasibility and safety of the experiment, Folk was joined in the cold room by two soldiers in tests designed by Griffin to determine how fast troops should run to maintain a safe body temperature in the extreme cold. Having read about military barracks catching fire in wintry environments, Griffin and Folk studied the balance of heat loss and gain during cold exercise in order to determine as well what emergency garb was reasonable to wear when escaping such a danger. They found that the effects of cold weather could be offset by jogging at seven

---

[45] Donald Griffin to Karl Lashley, 7 March 1944, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

[46] G. Edgar Folk, "The Harvard Fatigue Laboratory: Contributions to World War II," *Advances in Physiology Education*, Vol. 34, No. 3 (September 1, 2010): 119-127. Much of Harvard's archival record of the Fatigue Laboratory remains inaccessible to researchers due to Harvard's human subject privacy policy concerning its archives.

[47] Donald Griffin, "Projects under Consideration – Electrically Heated Clothing" [Unpublished report], Series 1.5, Box 12, Folder 112, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

miles per hour wearing just woolen underwear, and documented their findings in a report to the Quartermaster General and the Army Air Forces.

Other wartime research at the Fatigue Lab concerned the optimal distribution of heat in the electrically insulated suits worn by the crews in B-17 bombers. Griffin—"the most imaginative researcher at the Fatigue Laboratory," according to Folk—designed an experiment and a special piece of electrical equipment that allowed him to adjust the temperature in different parts of an electric suit using a row of rheostats.[48] Their goal was to determine how quickly cold conditions led to discomfort in different regions of the body, and how best to distribute external sources of heat to offset the negative physiological effects of extremely cold temperatures (the loss of manual dexterity, for example). One of the major problems of heated clothing involved the uneven distribution of heat throughout the body, which kept the test subjects from reaching "thermal equilibrium." Griffin and Folk were only able to measure the loss of stored heat approximately and generally, since heat loss varied greatly depending on which part of the body was measured. Griffin took a technical approach to this problem, designing a special suit that could control the flow of electric heat to different parts of the body independently, thus keeping the subject in a total equilibrium.[49] Once again from the cold room, Folk donned the special suit and reported where his body felt too cold or too hot, while Griffin raised and lowered the temperature in the various compartments of the suit. The tests relied not only on thermo-physiological measurements, but subjective feedback as well, for the cold-room subjects informed the researchers where they felt most

[48] G. Edgar Folk, "Harvard Fatigue Laboratory," p. 121-122.
[49] Donald Griffin, "Projects under Consideration – Electrically Heated Clothing" [Unpublished report], Series 1.5, Box 12, Folder 112, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

uncomfortable given a range of different activities. The psychological and physiological effects of cold were also quantified objectively via tests that measured factors such as mental fatigue and mechanical dexterity. Folk and Griffin reported their findings to the Quartermaster's office and to engineers at General Electric, who designed new suits using Griffin's specifications. According to Folk, "we felt inspired by the knowledge that our aviators would be wearing suits like these, heated to the temperatures determined by us, in their life-and-death missions in the war."[50]

Another exciting new area of sensory perception technology involved infrared night vision, which Griffin worked on toward the end of the war. Beginning in mid-1944, he worked on this technology with physiologist George Wald and biochemist Ruth Hubbard back at Harvard's Biological Laboratories. The team addressed an important problem concerning top-secret night vision devices, which converted infrared light into visible images for American soldiers hunting their enemies in darkness. A major problem stemmed from the goggles' emission of an infrared "searchlight"—presumably invisible to the human eye—that was supposed to illuminate the enemy surreptitiously. However, it was quickly discovered that the searchlight produced a faint red glow that was ever so slightly detectable to the naked eye, and thus blew its cover (and that of the American soldier) amid the darkness of night. Back in the biology labs building, Griffin and his team conscripted and tested various filters designed by engineers at the EAL, leading to the redesign of goggles that lacked this security breach.[51] Although this highly classified research was not circulated in an OSRD report, Griffin's team did publish aspects of their findings just after the war. In a short article, they documented the spectral sensitivity of

[50] G. Edgar Folk, "Harvard Fatigue Laboratory," p. 121.
[51] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 76.

human vision to low levels of infrared radiation, demonstrating for the first time that the human eye was capable of observing a narrow range of the infrared spectrum.[52] Not surprisingly, their report made no mention of the top-secret military technology that had precipitated this discovery.

While these wartime investigations seem to have only tenuous connections to Griffin's work on bat orientation, it is important to consider that the bulk of his research concerned fundamental problems of subjectivity, such as the relationship between sensation (sensory physiology) and perception (psychology). This line of inquiry also entailed approaching the transmission of sound, radio signals, and communication in general as a form of information processing. PAL's articulation tests showed that communication was not simply a matter of coupling an adequate stimulus with a sensory mechanism, but rather a complex web of factors that included the intelligibility of certain linguistic elements, the role of attention and fatigue in auditory perception and signal processing, and the role of learning as subjects became more familiar with auditory cues. In cases where the physical stimulus and the sensory physiology of the listener remained identical, for example, auditory perception improved over the course of repeated testing. PAL's psychophysical research therefore served as a challenge to mechanistic understandings of perception and information processing, and championed the importance of the "human element" (attention, awareness, learning) in perception.

Griffin's wartime work exposed him to a variety of different scientific and practical problems. Additionally, the steady influx of new technologies must have been truly exciting for Griffin, a "gadget man," who took advantage of such developments in

---

[52] Donald Griffin, Ruth Hubbard, and George Wald, "The Sensitivity of the Human Eye to Infra-red Radiation," *Journal of the Optical Society of America*, Vol. 37, No. 7 (July 1947): 546-554.

his research and experimental design. His experience at the Fatigue Lab, for example, further cultivated Griffin's ability to approach problems of sensory physiology from a technical standpoint. Moreover, the fact that he was free to design his own experiments and to develop or modify existing technologies in the process yielded important experiences for developing an experimentalist mindset early in his career.

Working with scientists at PAL and EAL, Griffin also learned a great deal about the physical properties of sound waves and transmission, in addition to its information-carrying capacity, the use of electronics to visualize sound, and technologies that converted sound waves into electromagnetic radiation both for the purposes of scientific study. Griffin's exposure to newly developed and technically sophisticated audio equipment also provided him with new insights into the physical properties of sound and high-frequency signaling. As his wartime research wound down, Griffin hit the ground running on more in-depth research into the physical properties of bat sounds and the physiology of bat vocalizations themselves. He was subsequently able to resume his Junior Fellowship and "apply to bats what I had learned about acoustics" from his colleagues and research experiences at PAL and EAL.[53] But before we return to bats, it is necessary to highlight one more important area of wartime research that shaped how Griffin understood bats and their behavior: radar, sonar, and the military technologies of remote sensing.

[53] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 76. Francis Wiener, an expert on physical acoustics, collaborated with Griffin and others in PAL on their voice communications research. Wiener served as an important resource for Griffin after the war, technically advising him on his high-frequency microphone and oscilloscope setup for recording and analyzing bat sounds.

Radar in the Air

In November of 1944, Griffin wrote a brief letter to physicist Frederic V. Hunt (1905-1972), an expert on sonar, and director of Harvard's Underwater Sound Laboratory (HUSL).[54] In the decades surrounding World War II, Hunt was one of the most widely recognized authorities on underwater sound, and probably the single most influential American scientist working on sonar technology.[55] Griffin explained to Hunt, "in discussing how bats guide their flight I have felt the need for a single word to describe their method." "Echo sounding" was inadequate, as it was already widely in use to describe the specific function of fathometers measuring the depth of the underwater floor. Griffin desired a new term that could broadly encompass a wider range of phenomena, of which bat echolocation constituted a particular biophysical instance. He further explained, "To describe the bats' method of orientation I have therefore coined the word 'echolocation,' defined simply as the locating of obstacles by means of echoes. The purpose of the enclosed note is to point out that this concept can equally well be applied to a wide range of diverse phenomena from a blind man's cane tapping to underwater sound devices or radar."[56] Hunt was less enthusiastic and recommended against coining such a term, which he felt lacked "euphony," but Griffin nevertheless persisted in popularizing the neologism. His former collaborator Robert Galambos did not share Hunt's reservations, urging Griffin to publish the term and to pursue the ideas that it embodied: "The echolocation paper is a very good idea. I've asked some people about it

[54] Hunt coined the term SONAR for its phonetic similarity to the term RADAR (RAdio Detection And Ranging). Thus SONAR essentially meant "sound radar," and applied to a wide range of technologies and methods for underwater detection. After it became widely adopted by the Navy, the acronym was retroactively held to stand for "SOund Navigation And Ranging."
[55] John V. Bouyoucos, "Frederick V. Hunt [Obituary]," *Physics Today*, Vol. 25, No. 7 (Jul. 1972): 69-70.
[56] Donald Griffin to F.V. Hunt, 11 November 1944, Series 1, Box 4, Folder [Correspondence - Hoc-Hut], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

and while none are tremendously enthusiastic, I am, and I congratulate you on the concept and urge you to go thru with it."[57] When Griffin suggested that he include Galambos as a co-author, his colleague demurred, "I really think you should take echolocation for your own […] after all it is solely your concept, [and] my contribution, as you must admit, is absolutely nil."[58] In December of 1944, Griffin published his term in an article in *Science*.[59]

In his echolocation article, Griffin briefly recapitulated the history of Hartridge's auditory theory of bat orientation and the experiments that he and Galambos had performed in confirming it via the detection of ultrasonic echoes. He then surveyed several instances of echolocation that utilized "the same fundamental process," two of which were physiological (facial vision in blind persons, and bat orientation), and the remainder technological (fog-horns, fathometers, altimeters, sonar, and radar).[60] Sonar and radar, of course, were still secretive military technologies, but the basic features of radar had recently been disclosed to the public in the spring of 1943.[61] In fact it had occasionally been referred to publicly before that, especially in Europe, where radar was celebrated for its pivotal role in the early-warning detection system that alerted the R.A.F.

[57] Robert Galambos to Donald Griffin, 24 August 1944, Series 1, Box 4, Folder [Corr- Galambos], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

[58] Robert Galambos to Donald Griffin, [Undated 1944], Series 1, Box 4, Folder [Corr- Galambos], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. Emphasis in original.

[59] Donald Griffin, "Echolocation by Blind Men, Bats, and Radar," *Science*, Vol. 100, No. 2609 (Dec. 1944): 589-590.

[60] Griffin had learned about facial vision in blind persons at some point in early 1944, a few months before psychologists Michael Supa, Milton Cotzin, and Karl Dallenbach published an important paper on the subject. Michael Supa, Milton Cotzin, and Karl Dallenbach, "'Facial Vision': The Perception of Obstacles by the Blind," *The American Journal of Psychology*, Vol. 57, No. 2 (Apr. 1944): 133-183. Griffin mentioned that work in a letter to Karl Lashley in March, 1944: Donald Griffin to Karl Lashley, 7 March 1944, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

[61] O.E. Buckley, "[Radar]," *Bell Laboratories Record*, Vol. 21 (Jun. 1943): 333. Several major news outlets picked up this story and widely disseminated information about radar.

to incoming Luftwaffe attacks during the Battle of Britain.[62] Aware of its scientific and cultural significance, Griffin explained that "it would be presumptuous for a biologist to discuss radar in detail," but he nevertheless thought it was important to frame its basic principles in terms of their resemblance to the physiological basis of bat navigation.[63] Without naming it directly, he also hinted at the use of sonar in submarine detection, an even more clandestine technology that had not yet been made public "for obvious reasons."[64]

As Griffin later explained, one motivation for coining the term was to combat resistance to the very idea that bats were capable of such a complex and strange way of life. He recalled that at the 1940 American Society of Zoologists annual meeting, the acclaimed sensory physiologist Selig Hecht, upon hearing that bats navigated their flights via ultrasonic echoes, apparently grabbed Galambos by the shoulders and shook him, "complaining that we could not possibly mean such an outrageous suggestion."[65] Because the bat's way of life was so utterly strange and different to that of humans, Griffin thought that by calling attention to the fundamental similarities of echolocation in bats

---

[62] For instance, as early as 1941 in the *New York Times* the Navy took out an advertisement specifically seeking radar engineers: "Navy Seeks Radio Technicians," *New York Times*, 18 November 1941, p. 8. In September 1940, the British sent a special envoy—the "Tizard Mission"—to discuss developments in radar research with members of the U.S. military. Up until that point, research in both countries had been pursued independently. On the role of radar in World War II, see: Louis Brown, *Technical and Military Imperatives: A Radar History of World War II* (Philadelphia: Institute of Physics Publishing, 1999), especially p. 107-122.

[63] Donald Griffin, "Echolocation by Blind Men, Bats, and Radar," *Science*, Vol. 100, No. 2609 (Dec. 1944): 589-590.

[64] Donald Griffin, "Echolocation by Blind Men, Bats, and Radar," *Science*, Vol. 100, No. 2609 (Dec. 1944): 589-590. Although the basics of radar technology were disclosed to the public in early 1943, details of sonar were much more secretive at the time. The reasons for this are not entirely clear, but a major reason for making public the details of radar was that much information about it had simply leaked out. Moreover, the British and Germans (among other nations) had independently developed radar, and it was widely discussed in European newspapers, even though most references in American sources were veiled until 1943.

[65] Donald Griffin, "The Early History of Research on Echolocation," in *Animal Sonar Systems*, eds. Rene-Guy Busnel and James F. Fish, p. 1-8 (New York: Plenum Press, 1980), p. 3. Hecht was a strong admirer of Jacques Loeb's mechanistic epistemology, and thus thought of animals as simple and machine-like.

and radar in his 1944 article, skeptics such as Hecht would be more willing to accept the validity of their discovery. The real significance of the term lay in its potential for guiding future research: "Unsuspected forms of echolocation may be found in nature or developed by human technology, and the use of a single unifying term can help clarify our ideas and stimulate such future developments."[66] Thus, not only were these similarities interesting in and of themselves, but Griffin thought that subsuming the technological and physiological phenomena under a more generalized conceptual framework would yield new discoveries. As it turns out, this supposition was correct, for in the years following the war Griffin's research on bat echolocation revealed startling new features, many of which were shared by its technological analogs.

Griffin's coining of the term echolocation also served two other, perhaps less significant, functions. First, it essentially guaranteed that moving forward, the discovery of ultrasonic bat orientation would be mainly attributed to him.[67] As we have seen in the previous chapter, it was actually Hamilton Hartridge's auditory hypothesis that Griffin and Galambos had confirmed via their obstacle avoidance experiments (which were based on the earlier work of Walter Louis Hahn). While Hartridge was unaware in 1920 that bats produced ultrasonic echoes, he nevertheless suspected that they might and had suggested so. Moreover, just a few years after Griffin's and Galambos's work, the Dutch physiologist Sven Dijkgraaf independently suggested in 1943 that bats oriented themselves via the echoes of their faintly audible clicking noises.[68] Dijkgraaf, who was

---

[66] Donald Griffin, "Echolocation by Blind Men, Bats, and Radar," *Science*, Vol. 100, No. 2609 (Dec. 1944): 589-590.
[67] This was not an explicit purpose of his, but it did ultimately lead to Griffin's name becoming inextricably linked to the discovery of echolocation.
[68] Sven Dijkgraaf, "Over een merkwaardige functie van den gehoorzin bij vleermuizen [On a remarkable function of the sense of hearing in bats]," *Verslagen Nederlandsche Akademie van Wetenschappen Afdeeling Naturkunde*, Vol. 52 (1943): 622-627. After learning about Dijkgraaf's work, Griffin later

isolated in the German-occupied Netherlands during the war, was unaware that bats produced ultrasonic sounds, but demonstrated via experiments quite similar to Griffin and Galambos that the bats' clicking sounds correlated with their ability to avoid obstacles. Dijkgraaf theorized that the echoes of these clicks helped bats guide their flights. Despite the important contributions of these other twentieth-century scientists, and the fact that Spallanzani and Jurine had suggested a form of the auditory hypothesis nearly 150 years before, by coining the term "echolocation" Griffin attached his name to the permanent solution to the "bat problem" for posterity.

Finally, the term "echolocation" served a pragmatic function, since it described "an important and general process for which one otherwise requires long phrases or whole sentences."[69] Throughout his several publications between 1938 and 1942, Griffin had never landed firmly on an adequate term or phrase that could succinctly capture the phenomenon or its significance. While he most often characterized the ultrasonic basis of bat orientation with the passively constructed and nebulous phrase, 'obstacle avoidance,' he also fumbled around with other terms such as the 'auditory hypothesis,' 'Hartridge's hypothesis,' the 'ultrasonic hypothesis,' 'echo-sounding,' and so on. He also occasionally referred to it as the 'supersonic' or "SS" hypothesis, but dropped that in 1946, when the term supersonic came to designate the speed of new aircrafts that were capable of breaking the sound barrier.[70] In echolocation then, Griffin had crafted a succinct and

showed that the clicks were merely ancillary audible components of the bat's orientation cries. The more intense and higher frequency sounds—which were almost always accompanied by the audible click—were the cues actually used for orientation. Dijkgraaf evidently had a better sense of hearing than Griffin, who was never able to hear the audible components of orientation cries.

[69] Donald Griffin, "Echolocation by Blind Men, Bats, and Radar," *Science*, Vol. 100, No. 2609 (Dec. 1944): 589.

[70] After this point, sound above the audible frequency range of humans became known as "ultrasonic."

powerful metaphor, capable of serving multiple functions and merging different clouds of associations related to both the military and sensory physiology.

Echolocation, insofar as it came to be conceived of as an interactive mode of perception by which bats acquired information about various features of their environments, was in fact a far cry from obstacle avoidance. As Griffin initially understood bats, avoidance behavior was the product of a specific and automatic physiological mechanism. Echolocation, on the other hand, was construed as a more general method, or tool, that bats had evolved to negotiate a wider range of tasks in their daily lives. In fact the phrases themselves delimit separate levels of inquiry: whereas obstacle avoidance refers specifically to the ability of bats to avoid airborne collisions, echolocation describes a general physiological process, or mode of perception, applicable to a wider and undefined range of behaviors and activities.

Consider Griffin's description of his early work on obstacle avoidance in a letter to James Brown Fisk, the physicist and Harvard Junior Fellow who, along with G.W. Pierce, had participated in the initial orientation experiments in 1938. Those experiments revealed that bats emitted ultrasonic sounds, although apparently not for the purpose of aerial orientation. In 1940, after Fisk had moved from Harvard to Bell Labs to work on increasing the range and accuracy of military radar systems, Griffin brought him up to speed on additional orientation experiments.[71] "Apparently we jumped to conclusions two years ago as far as the relation of the supersonic chirps to obstacles was

[71] William H. Doherty, "James Brown Fisk: 1910-1981," *Biographical Memoirs of the National Academy of Sciences of the United States* (Washington, DC: 1987), p. 99-101. This was part of a huge undertaking to create centimetric radar utilizing ultra-high frequency microwaves, which was more powerful and accurate than radio-wave radar systems. British engineers had already found a way to generate the powerful microwaves for use in RDF/radar systems, and they famously shared this information with American scientists during the Tizard Mission in September of 1940. At Bell Labs, Fisk initially worked on increasing the power of generators that were necessary to produce the powerful microwave signals of centimetric radar.

concerned."[72] Those overly conservative conclusions were revised in light of Griffin's and Galambos's more thorough study of obstacle avoidance: "under these circumstances the bats keep up their high frequency notes while flying about, and seem to emit a specially loud and rapid volley of chirps just as they approach the wires […] The general conclusion is that hearing of sound reflected or scattered from the wires is an important mechanism enabling the bat to avoid them."[73] Bearing in mind that by the time he wrote those words, Griffin had ceased most of his experimental work on bats, it is interesting to contrast that description of bat biophysics to one written just a few years later in 1944, after he had coined the term echolocation.[74] Regarding the bat's use of echolocation while in flight, Griffin explained: "The bat is essentially locating objects in space by means of echoes…In its echolocation of obstacles the bat must do more than merely measure the distance to the obstacle; he must also localize the direction from which the echo is returning."[75] Griffin further explained that other abilities based on echolocation were likely to be discovered, including "the ability of bats to find the relatively small entrances to caves in the midst of dense woods."[76]

Conceptually and linguistically, echolocation was construed as a more general perceptual ability, used interactively by the bat to investigate its environment, as opposed to the restricted mechanism of obstacle avoidance. By 1946, Griffin's understanding of echolocation had further evolved: "This remarkable method of perception takes the place

---

[72] Donald Griffin to James Fisk, 6 March 1940, Series 1, Box 3, Folder [Corr – F], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[73] Donald Griffin to James Fisk, 6 March 1940, Series 1, Box 3, Folder [Corr – F], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. Note the inherent passivity implicit in the phrase "hearing of sound."
[74] Donald Griffin, "How Bats Guide their Flight by Supersonic Echoes," *The American Journal of Physics*, Vol. 12 (1944): 342-345.
[75] Donald Griffin, "How Bats Guide their Flight by Supersonic Echoes," p. 345.
[76] Donald Griffin, "How Bats Guide their Flight by Supersonic Echoes," p. 345.

of vision for the bat […] this process is the chief mode of perception available to bats, and in this way they obtain most of their information about their surroundings. The process is so distinct from other types of perception that I have called it 'echolocation,' or the location of objects by means of their echoes."[77] Thus by the end of the war, echolocation had been generalized to indicate a complex form of interactive perception, which served a greater range of needs for bats both in orientation and in extracting information from objects within their environments.

Griffin wasted little time putting his new term to work, publishing a more technical article in the *American Journal of Physics* at the behest of its editor, Duane Roller.[78] Therein Griffin emphasized aspects of echolocation that would be most interesting to physicists, such as the acoustic properties of bat signals (frequency, duration, length).[79] He did well to show its relevance to physicists, whose help he would indeed come to rely on for understanding the biophysics of bat sounds. In fact, earlier he had worried that his rudimentary understanding of physical acoustics would engender skepticism among physicists who learned about this work. In a 1941 letter to his friend and colleague Harold Hitchcock, for example, he pondered:

> In general, our idea is that the bats emit sounds above our frequency range (maximum intensity usually at 50 kilocycles) and that some of this sound comes back from the wires to them, is heard, and the source of the reflected sound, i.e. the obstacle is localized by the same sort of localization method whcih [sic] is used by other mammals for sounds of frequencies audible to them […] The physicists will probably jump down your throat if you talk about reflection from wires 1 mm. in diameter of a sound with a wave-length of 6 or 7 mm. Perhaps scattering is the better word. I have been after several physicists to advise me about the theory of this, but they all get very vague. As far as I can see, sound

---

[77] Donald Griffin, "Mystery Mammals of the Twilight," *National Geographic*, Vol. 90 (Jul. 1946): 117-133.
[78] Duane Roller to Donald Griffin, 6 May 1944, Series 1, Box 8, Folder [Corr – Publishers - Other], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[79] Donald Griffin, "How Bats Guide Their Flight by Supersonic Echoes," p. 342-345.

> waves being a longitudinal vibration (molecules moving in the direction of the propagation of the wave) should not be bothered particularly by the reflecting object being smaller than the wave-length as light waves are. If any of your physicists are really interested in this I'd be glad to send them all the dope we have in hopes that they might have some ideas illuminating to a poor ignorant biologist.[80]

The physical properties of sound (e.g., wavelength, scattering versus reflection) were thus crucial elements of echolocation, determining how and for what purposes bats might use it. However, before Griffin's wartime research, he had little exposure to physical acoustics. The 'all hands on deck' mentality of the war thus yielded crucial opportunities for biologists such as Griffin to increase their knowledge of physics and acoustical engineering.

Griffin took the connection between bats and radar seriously. While bat brains obviously did not contain exact equivalents of the electronic apparatuses involved in radar, they did "possess physiological mechanisms which guide their flight in much the same way."[81] The ability of bats to navigate in total darkness, he explained, "is achieved by using the working equivalents of such modern electronic devices as echo sounders, absolute altimeters and radar." Despite their physical differences, the signals are in fact employed in a similar capacity. While bat auditory physiology handles the binaural localization of sound (via differences in phase and intensity between echoes received by two ears separated in space), triangulated radar stations similarly localize the sources of radar reflections via temporal and energy differences. Griffin concluded the article by

[80] Donald Griffin to Harold Hitchcock, 23 February 1941, Series 1, Box 5, Folder 61, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[81] Donald Griffin, "How Bats Guide Their Flight by Supersonic Echoes," p. 342.

observing that bats were thus capable of achieving "results which I think any radar engineer might envy."[82]

Surprisingly, he was not the first to observe the now-ubiquitous parallels between radar and bats. That honor goes to the biologist Rachel Carson, at the time a budding science writer who would later become famous for warning against overuse of pesticides in her book *Silent Spring* (1962).[83] In November of 1944 she scooped Griffin in a short article for *Collier's Weekly*, "The Bat Knew it First."[84] Although she did not coin a new term to connect the related phenomena, Carson emphasized the important parallels between radar and bats: "As everyone knows, radar detects approaching planes or other objects in the sky by filling the air with a series of high-frequency radio waves, then receiving the echo that bounces back from anything in the path of the signals. The bat's method is very similar. Instead of radio waves, he sends out a staccato series of high-pitched cries."[85] At the time, radar was quickly seeping into the public consciousness, especially for the noteworthy role that it had played in aiding the British defense during the Battle of Britain in 1940.[86] Carson summarized Griffin's and Galambos's obstacle avoidance experiments, and then speculated on the evolutionary origins of the bat's counterpart of radar. While radar technology was indeed a modern marvel, Carson noted that bats had "perfected and used the counterpart of radar millions of years before man laboriously developed it."[87]

---

[82] Donald Griffin, "How Bats Guide Their Flight by Supersonic Echoes," p. 342-345.
[83] Rachel Carson, *Silent Spring* (Boston: Houghton Mifflin, 1962).
[84] Rachel Carson, "The Bat Knew it First," *Collier's Weekly* (November 1944): 24.
[85] Rachel Carson, "The Bat Knew it First," p. 24.
[86] Louis Brown, *Technical and Military Imperatives: A Radar History of World War II* (Philadelphia: Institute of Physics Publishing, 1999).
[87] Rachel Carson, "The Bat Knew it First," p. 24.

While Carson correctly observed that by late-1944 public knowledge of radar was ubiquitous, that was certainly not the case when the U.S. entered the war. At Harvard and MIT in the early-1940s, however, excitement about radar and sonar was widespread, as scientists and engineers worked on various wartime projects to develop and improve the technology. F.V. Hunt's Underwater Sound Laboratory, for example, worked on the application of sonar to military weapons and navigation, while down the road at MIT, the Radiation Laboratory became the nerve center for America's burgeoning radar super-organism. Between January 1943 and June 1946 alone the OSRD doled out contracts in excess of $120 million for radar-related projects.[88] In addition to the Rad Lab, dozens of smaller teams worked on projects indirectly related to radar. Researchers at the Psycho-Acoustic Laboratory, for example, tackled problems that explicitly dealt with improving military communications concerning the dissemination of radar-based information, and integrating that data into the chain-of-command. At PAL, Griffin certainly would have gained a basic familiarity with radar and its principles, although he was probably already aware of it based on conversations with his colleagues G.W. Pierce, James Fisk, and Harold Edgerton, among others, all of whom worked on radar and/or sonar related research at the time.[89]

While the basic principles of radar would have circulated amongst scientists and engineers on Harvard's campus before it was made public, specifics about the technology and new areas of development were no doubt shrouded in secrecy. Moreover, before entering the war American radar technology was to a degree still in its infancy, relying on

[88] Irving Stewart, *Organizing Scientific Research*, p. 92-94.

[89] There is also a strong chance that new wartime technologies such as radar were discussed at informal gatherings of scientists within Harvard's interstitial groups such as the Society of Fellows, of which Griffin was a junior member beginning in 1942.

the relatively weak radio-wave based signals in devices such as the Navy's CXAM and the Army's SCR-270.[90] These radars, like the British "chain home" (CH) system, were essentially early-warning systems: their limited range (about 150 miles) and accuracy meant that they were good at detecting the presence of incoming enemies or obstacles on the horizon, but not for much else.[91] For example, with poor angular resolution, a squadron of dozens of incoming airplanes would appear as a single fuzzy blip on the oscilloscope screen. Two planes that were within six kilometers of one another would similarly appear as a single blip.[92] Similarly, radar navigation systems to help guide planes to remote targets were just being developed. The several pieces of equipment required by radar were also large, heavy, and thus confined to ground-based stations or large ships—airborne radars were also in the early stages. Thus, one of the major efforts in the early-1940s was to develop smaller airborne radars, and to increase the precision of radar by converting their signals to a more powerful microwave system.[93]

By this time most operational U.S. radars were still relatively low-powered and effective at relatively short ranges, relying on radio-wave signals with meter-long wavelengths. American engineers knew that radar signals utilizing quick bursts of short-wave, high-frequency microwaves would yield greater target resolution, but they simply lacked instruments capable of generating these high energy levels. This was a crucial

---

[90] For more on the development of radar, see Louis Brown, *Technical and Military Imperatives: A Radar History of World War II* (Philadelphia: Institute of Physics Publishing, 1999); Mark Denny, *Blip, Ping, and Buzz* (Baltimore: Johns Hopkins University Press, 2007).
[91] Mark Denny, *Blip, Ping, and Buzz*, p. 8-36. For example, they could not finely discriminate targets, nor act as effective guidance systems for accurate navigation. In 1939 the U.S. and German radars were more advanced than the British, but the Brits' well-coordinated chain home system nevertheless played a crucial role in detecting approaching German Luftwaffe squadrons. The efficient coordination and substantial manpower was enough to overcome the technological shortcomings of the primitive CH units. Mark Denny, *Blip, Ping, & Buzz*, p. 22-36.
[92] Mark Denny, *Blip, Ping, and Buzz*, p. 8-15
[93] Mark Denny, *Blip, Ping, and Buzz*, p. 38-39.

problem, because the amount of reflected energy that returns to a radar receiver falls off by a factor of four. Hence doubling the range of the radar reduces its signal power by a factor of 16, yielding poor target resolution.[94] In fact it was not until September of 1940, when British science and military ambassadors came to the U.S. in the famous Tizard Mission, that the Americans learned how to effectively generate these high-powered, shortwave signals. Although the British CH radar system was less sophisticated than some American radars, the Brits had invented cavity magnetrons that were capable of generating powerful microwave bursts: the crucial missing piece for newer microwave radars. Also known as centimetric radar, given that their signals relied on microwaves with a wavelength of 10 centimeters or less, these devices were made possible by the infusion of British intelligence. The Tizard Mission took place over the course of three months in the fall of 1940, with meetings at offices in Washington DC, MIT, and Bell Labs, where British scientists showcased the latest in radar capabilities, and similarly were made privy to some, but not all, American developments. Immediately thereafter, MIT's Radiation Laboratory was set up in order to produce the cavity magnetrons and integrate them into new microwave radar designs. Over the course of the war, radar technology was constantly improved, as the Americans mass-produced microwave radars, developed new Plan Position Indicators (PPI) that displayed radar data on electronic maps, and developed "tunable" magnetrons that were able to adjust the frequency of radar signals in order to circumvent jamming by the enemy.[95]

---

[94] Mark Denny, *Blip, Ping, and Buzz*, p. 48.

[95] Mark Denny, *Blip, Ping, and Buzz*, p. 43-44. The other major innovations are too numerous to list; suffice it to say, there was an explosion of innovation in radar technology in just a few short years. Aside from the Manhattan Project, no other wartime technology received more attention, manpower, or financial resources.

Excitement about radar at Harvard—especially for biologists—increased tremendously in July of 1942, when the Radio Research Laboratory (RRL) under the direction of Frederick Terman was moved from MIT to the top floor of Harvard's Biological Laboratories building.[96] Of the $24,500,000 spent on radar countermeasures during the war, two-thirds—$16,000,000—went to the RRL, whose main task was to develop both offensive devices and methods to jam enemy radars, and defensive measures to circumvent enemy jamming.[97] Initially employing 110 people, Terman's group added a rooftop annex as it expanded to 205 employees by October of 1942. By August of 1944 it had grown to 810 people, adding yet another annex behind the biology building.[98] Among the dozens of countermeasure devices and techniques developed by the RRL during the war, the most significant was the airborne electronic jamming method designated "Carpet," which played a crucial role in disrupting German Würzburg radars.[99] Since the returning echoes of radar signals were relatively weak, scientists and engineers found that they could effectively jam them by sending out stronger signals that overshadowed these echoes. Moreover, by developing airborne jammers that could be tuned the same frequency of enemy radars, jamming was highly effective and

[96] The RRL had been set up separately from the Rad Lab in March of 1942, and then quickly moved to Harvard because of secrecy concerns. Apparently too many people had access to the huge Rad Lab, which eventually grew to over 4,000 employees by the end of the war. James P. Baxter, *Scientists Against Time* (Boston: Little Brown and Co., 1946), p. 159.
[97] James P. Baxter, *Scientists Against Time*, p. 186-188. Baxter also notes that a bit of an informal arms race developed between scientists at the Rad Lab and at the RRL, as they constantly made improvements to their devices in order to thwart each other's jamming and counter-jamming efforts. James P. Baxter, *Scientists Against Time*, p. 187.
[98] Accounts differ as to when the group moved into the Biology Labs building, either in March or July of 1942. Regardless, Griffin and others in Harvard's biology department would have witnessed the enormous growth of the RRL over the course of the war.
[99] The British had already developed a more widespread jamming technique known as "Window" or "Chaff," which consisted in scattering millions of aluminum strips, dropped from planes in the upper atmosphere. Outgoing radar signals bounced off these strips, returning a confusing array of reflected radiation that rendered radars useless for discriminating between actual enemy planes and the large swaths of aluminum floating in the sky. Tens of millions of pounds of aluminum foil were dropped over Europe during the war. James P. Baxter, *Scientists Against Time*, p. 163-164.

increasingly precise, and could be adjusted on the fly in case enemy radars were tuned to a different frequency.[100] Thus enemy signals were unable to cut through the noise of Carpet jammers, rendering their radars incapable of generating any form of useful information.[101]

This research was highly classified, and scientists such as Griffin who did not work in the RRL would not have known much detail. Nevertheless, rumors must have swirled amongst Harvard's biology department as the clandestine RRL group gradually colonized the Biology Laboratories building. Moreover, Griffin did have at least one friend who worked in the Radio Research Laboratory during the war. In early 1945, this unnamed individual helped Griffin analyze the finer properties of bat sounds using RRL equipment: "Photographing these bat cries was quite difficult, but with the help of a friend in the Radio Research Laboratory I borrowed a very bright cathode ray tube and a very fast film and lens. Pictures were taken at random when the bat was 'talking,'" and Griffin used them to examine the bat's signal in greater detail than he had before.[102] Evidently he became familiar with the RRL's equipment, for just after the Pacific campaign ended, he sought to acquire several electronic devices to aid him further in the analysis of bat cries.[103] Thus, although the connections between bat echolocation and radar were not yet paying obvious conceptual dividends, they were certainly beginning to show important practical parallels vis-à-vis the devices required to analyze their signals.

---

[100] In fact the most popular German radars, the Würzburgs, could not easily adjust the frequency of their signals. Thus, once Carpet started broadcasting its jamming signals, German radars were basically blind.
[101] James Baxter, *Scientists Against Time*, p. 165-166.
[102] Donald Griffin to G.W. Pierce, 5 February 1945, Series 1, Box 8, Folder 89, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[103] Donald Griffin to Jeffries Wyman, 4 September 1945, Series 1, Box 12, Folder [Corr - Wie-Wy], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

It might be tempting to surmise that Griffin's work on bat echolocation had direct lines of influence on radar research, despite the fact that high-energy microwave signals are fundamentally different—from the standpoint of physics—from mechanical sound (pressure) waves. There is no evidence, however, that the "radar people" looked to bats for technological inspiration, but that fact did not keep certain individuals from suggesting so. Thomas Barbour (1884-1946), a distinguished naturalist and director of Harvard's Museum of Comparative Zoology from 1927 until his death in 1946, would claim just that. In 1945 Barbour wrote a short article about bats for *The Atlantic*, in which he claimed that Griffin's and Galambos's work had shown that "in other words, the bat is a miniature, individual radar installation which has provided many a valuable hint to the geniuses who have been working on supersonic direction and perception during the last year or two. This is a clear illustration that no one can ever tell where the study of natural phenomena, however improbable it may appear from a utilitarian point of view, may end."[104] Amusingly, Griffin wrote to Barbour explaining that his batty work contributed little to wartime research on radar: "The final item is the implication that radar owes part or all of its development to our work with bats. We must disclaim any such credit, however; at the time that we were still accumulating data on bats, the British were already shooting down Goering's bombers with the aid of highly perfected radar installations."[105] Griffin's rebuke notwithstanding, Barbour stubbornly reiterated his claim, explaining to his younger colleague, "I have been told so often how much your

[104] Thomas Barbour, "Bats," *The Atlantic*, Vol. 175, No. 6 (June 1945): 90-93.
[105] Donald Griffin to Thomas Barbour, 18 June 1945, Series 1, Box 1, Folder [Corr – Ba-Be], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

work aided in the elaboration and development of the progress in radar that I am not in the least inclined to withdraw any of that."[106]

Those facts notwithstanding, Griffin firmly believed that radar researchers did have much to learn from bats, and it frustrated him that none had taken the connection seriously. In March of 1944 he groused to his doctoral advisor Karl Lashley:

> This in turn leads into the question I have often asked myself about the bats' echo sounding; why haven't the radar people really studied the bats' signal (which has a very peculiar time pattern - very sharp, short bursts repeated as fast as 50 per second)? Since the bats have had 50,000,000 years to evolve an acoustic radar, it would seem likely that some good features might be discovered from a thorough analysis of their methods. As far as I can learn this hasn't been attempted. […] I have had no time free from earphone sockets or electrically heated gloves to do more than speculate along these lines.[107]

For Griffin, echolocation was an interactive metaphor: one could learn about bats by thinking of them in terms of biological radar or sonar, and similarly, one could improve radar by learning how bats employed their physiological analogs. And in fact the power of the metaphor to illuminate new lines of inquiry was one of Griffin's motivations for coining the term in the first place.

As to the influence of sonar, that research was even more clandestine than radar, and Griffin's ties to Harvard's Underwater Sound Laboratory were more tenuous. During the war, F.V. Hunt's lab was focused mainly on the development of weapons such as sonar-guided torpedoes and sonar-based weapons detection systems, so in addition to being more secretive, the work was not as directly appealing to Griffin.[108] Nevertheless, there is evidence that he sought the advice of sonar researchers including Hunt, and at

[106] Thomas Barbour to Donald Griffin, 20 June 1945, Series 1, Box 1, Folder [Corr – Ba-Be], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. Barbour's insistence is curious, but he never explicitly named the source of these rumors, so they remain unconfirmed.
[107] Donald Griffin to Karl Lashley, 7 March 1944, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[108] *Applied Acoustics in Subsurface Warfare* [Final Report], Harvard Underwater Sound Laboratory, OSRD (Cambridge, MA: HUSL, 1946).

one point Griffin visited the HUSL in order to test the ability of one of its hydrophones to discriminate the finer properties of bat sounds.[109] HUSL's hydrophone, however, was not sensitive enough for Griffin's purposes, and so he returned to G.W. Pierce's Cruft lab looking for better equipment.[110] Pierce himself was also well aware of sonar research, as his good friend and fishing buddy was none other than sonar pioneer Harvey C. Hayes, superintendent of the Naval Research Laboratory's sound division during the war.[111]

Griffin was also friends with Harold Edgerton, who had helped Griffin and Galambos take high-speed photographs and films during their obstacle avoidance experiments before the war. Edgerton was a pioneer in stroboscopic technology at MIT, and during the war he developed tools and methods for high-speed nighttime reconnaissance photography for the military. Edgerton also worked on sonar, and after the war he developed techniques for using "side-scan sonar" to photograph underwater geographic features that were of interest to the military.[112] Griffin called on him a few times for assistance in taking high-speed photographs of bat sounds displayed on Pierce's ultrasonic receiver and oscilloscope setup.[113]

Griffin's personal and professional network thus included several key individuals working on radar, sonar, and other military technologies. If he had questions about the basics of sonar, he was certainly in a position to have them answered, and the fact that he

---

[109] This visit was probably in 1944, although it could have been after the war. In writing to Hunt just before the publication of Griffin's echolocation article in December 1944, Griffin may have been motivated by a desire to pique Hunt's interest in bat research for the purpose of future collaboration.

[110] Donald Griffin to Francis M. Wiener, 10 August 1951, Series 1, Box 12, Folder [Corr - Wie-Wy], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. It may have been after his failed visit to the HUSL that Griffin turned to Radio Research Laboratory for equipment.

[111] David K. Allison, *New Eye for the Navy: The Origin of Radar at the Naval Research Laboratory* [NRL Report 8466], (Washington, DC: Naval Research Laboratory, 1981), p. 82.

[112] Paul Gray, "Harold E. Edgerton [Obituary]," *Physics Today*, Vol. 44 (1991): 126-128. On Edgerton's wartime work, see the Harold Edgerton digital collections: http://edgerton-digital-collections.org/

[113] Griffin used Edgerton's photographs of bats in flight for a *National Geographic* article in 1946. Donald Griffin, "Mystery Mammals of the Twilight," *National Geographic*, Vol. 90 (Jul. 1946): 117-133.

included references to it in his initial echolocation article attests to that fact. For his war years at Harvard, radar was in the air just as much as sonar was in the water, and after the war, Griffin applied what he had learned to bats.

Radar and sonar forever changed the way that Griffin understood bats. In several articles and book chapters written after the war, he discussed and compared echolocation in bats to its technological cousins. The comparison to radar also conferred a certain "wow" factor onto bats, since they were seemingly capable of feats achievable by the most sophisticated technologies of the day. In a 1946 article on bats for *National Geographic*, for example, Griffin invoked radar in order to underscore just how extraordinary the bat's way of life was: "The most spectacular example of echolocation is the modern miracle of radar, which sends out radio waves and measures the distance and direction of aircraft or other objects by the echoes of these waves." As a method of remote sensing, echolocation similarly afforded bats the ability to "see with their ears."[114]

In a later article, just as he was beginning to explore the possibility that bats hunted via echolocation, Griffin once again emphasized their fundamental connections to sonar and radar.[115] As he explained, "some say [bats] possess radar, and this is surprisingly close to the truth."[116] Although sonar, since it also employed sonic echoes, was a better comparison from the standpoint of physics, Griffin explained the importance of these parallels: "There are startling similarities between the bat's method and radar,

---

[114] Donald Griffin, "Mystery Mammals of the Twilight," *National Geographic*, Vol. 90 (July 1946): 134.
[115] Donald Griffin, "The Navigation of Bats," *Scientific American*, Vol. 138 (Aug. 1950): 52-55. Griffin also invoked facial vision in blind persons as a form of human echolocation. However, he tended to do this in passing, as a way to generate interest in the subject. Although he intended several times throughout his career to look into human echolocation in more detail, it always seemed to get put on the backburner in favor of battier projects.
[116] Donald Griffin, "The Navigation of Bats," p. 52.

not only in basic principles but even in some of the less obvious details."[117] Along with sonar, all three forms of echolocation employ "bursts of energy…in order to detect distant objects by means of echoes," and used shortwave, high-frequency signals to "permit the detection of smaller objects." Furthermore, they all utilize suppressing mechanisms in their receivers (in the case of bats, muscles that constrict in the inner-ear) to prevent damage from the intense outgoing signals. Finally, all three systems utilize energetic signals concentrated in time (short bursts or pulses) and in space (highly directional beams). These three forms of echolocation were therefore remarkably similar, and Griffin concluded the article by wondering, "had biologists understood a few decades earlier the methods by which bats orient themselves, might not the invention of radar and sonar have come sooner?"[118]

Hunting, Jamming, and Target Discrimination: Applying the War to Bats

Wartime research—especially involving psychoacoustics and radar—had important consequences for the elaboration of echolocation studies. Griffin would eventually ask new questions about echolocation in bats: do they use it for hunting insects? How effective is the bat's target discrimination? And is the bat's signal, like its radar analog, susceptible to jamming? These sorts of questions did not surface immediately or simultaneously. Instead, his wartime experience slowly influenced Griffin by inspiring a set of new ideas and questions via the echolocation metaphor, and a technical way of approaching bats as analogs to military technologies.

---

[117] Donald Griffin, "The Navigation of Bats," p. 54.
[118] Donald Griffin, "The Navigation of Bats," p. 54-55.

As his wartime research wound down, Griffin immediately returned to bats and the physical properties of their echolocation signals. The decision to return to bats—and to the nature of their signals specifically—was by no means random. His research on the properties of high-frequency sound and information processing at the Psycho-Acoustic Laboratory, as well as conversations with scientists working on other signal processing technologies for the military, led him to a new understanding about the information carrying capacity of sound waves. The physical properties of the echolocation signal, as radar and sonar showed, precisely determined the type and amount of information that could be acquired. Using methods that mirrored the analysis of radar signals on cathode ray oscilloscopes, Griffin set up equipment to visualize and analyze the finer details of bat sounds (spectrographs). His colleague and friend Francis Wiener (of the Electro-Acoustic Laboratory) assisted Griffin with the research and the equipment setup, which consisted of a condenser microphone, a cathode vacuum tube, and a volt amplifier to allow the sound waves to be viewed on an oscilloscope. One key piece of equipment, a DuMont model 247 oscilloscope, was purchased from the Radio Research Laboratory.[119] Through careful analysis, Griffin determined that bat signals consisted of a series of short pulses, and "rather than being broadband noise bursts, they were frequency modulated chirps sweeping downward by an octave during 1 or 2 msec."[120]

Griffin's postwar work surprisingly revealed that bats—or at least the *Myotis lucifugus* that he studied—emitted a frequency-modulated pulse that swept down a full octave over its duration. That is, the beginning of each pulse consisted of sound waves

---

[119] Donald Griffin, "The Supersonic Cries of Bats," *Nature*, Vol. 158 (July 13, 1946): 46-48. Some of the equipment was purchased through the Elisabeth Thompson Science Fund, and other pieces were on loan from the Psycho-Acoustic Laboratory.
[120] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 77.

whose frequency was much higher than those at the end of the pulse. Griffin was unsure of the reason for the sweep, but by analyzing the envelope form, its average pressure, and its duration, he would be able to get a better sense of the 'shape' of the bat's pulse.[121] This information was crucial for determining several aspects of echolocation, such as its effective range and the possibility that it could be used to discriminate the shape and texture of targets. He found that each burst of sound began at a frequency of 50,000 cycles per second and swept down to 20,000 cycles per second.[122] By visualizing the sound on an oscilloscope he found that the average intensity of each pulse was approximately 50 dynes/cm^2, which was indeed a very intense sound.[123] Similarly, he found that the bulk of the pulse's energy was emitted within a millisecond, and the entire pulse lasted slightly less than two milliseconds.[124] A pulse of such duration and intensity should theoretically allow a bat to echolocate objects at a distances no shorter than one foot, given the fact that it would take each pulse approximately 2 milliseconds to hit the target and return to the bat's ears as an echo. Objects closer than one foot away would return echoes that interrupted the emitted pulse before it had fully left the bat's larynx, and therefore echolocation at such distances would be ineffective.

---

[121] The envelope form is determined by tracing the peaks of each sound wave in the bat's pulse through time.

[122] The fact that the pulses never dipped below 20,000 cycles per second meant that no portion of the pulse was audible; the click sounds that Dijkgraaf had identified as orientation signals were therefore some ancillary byproduct of the orientation cries that resulted from the rapid nature of the pulse's production. Any acoustic energy below 20,000 cps created by this process was therefore unrelated to orientation activities. Donald Griffin, "The Supersonic Cries of Bats," p. 46-48.

[123] In a later article Griffin revised this estimate to 60 dynes, and offered helpful comparisons to demonstrate the intensity of bat signals: elevated trains produce sound at 10 dynes per centimeter squared, and the inside of combat planes averaged 100 dynes per centimeter squared. Griffin would have known this latter figure because of his work at PAL. Donald Griffin, "Measurements of the Ultrasonic Cries of Bats," *Journal of the Acoustical Society of America*, Vol. 22 (Mar. 1950): 247-257.

[124] Griffin and Galambos had initially determined in 1940 that the bat's pulse was about a tenth of a second; these later studies revealed that it was indeed much shorter than that.

It is unclear from whom and when Griffin learned that there existed an important correlation between the wavelength of echolocation signals and the size of objects that they could detect. Perhaps this was intuitively obvious despite his limited training in physics. It is also very likely that G.W. Pierce or James Fisk, both experts on physical acoustics, explained this to him in the late-1930s. At the very least Griffin was still worried about that problem in early 1941, when he wondered to his friend Harold Hitchcock how a physicist would react upon learning that bats detected wires 1mm in diameter via the reflection or scattering of sound waves that were 6-7mm long.[125] Nevertheless, the relationship between the wavelength and the target size was a central feature and problem in radar and sonar development, and so during the war, Griffin certainly would have had the opportunity to ponder this question.

A few years later Griffin published an even "more complete analysis" of bat signals, which led to some minor revisions of his earlier measurements.[126] He also detailed all of his methods and equipment—and offered tips for handling the bats in captivity—so that other interested scientists could replicate his experiments. Griffin emphasized the frequency sweeps, explaining that they were "one of the most important acoustical properties of these unusual sounds."[127] Although he was uncertain as to the role that the sweeps played in echolocation, Griffin drew on his knowledge of their role in radar, which employed frequency sweeps in order to avoid jamming their own echoes via outgoing signals: "It is tempting to speculate about the significance of this frequency modulation in the process of echolocation, especially in view of the use of frequency

---

[125] Donald Griffin to Harold Hitchcock, 23 February 1941, Series 1, Box 5, Folder 61, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[126] Donald Griffin, "Measurements of the Ultrasonic Cries of Bats," *Journal of the Acoustical Society of America*, Vol. 22 (Mar. 1950): 247-257.
[127] Donald Griffin, "Measurements of the Ultrasonic Cries of Bats," p. 251.

modulation in certain radar systems."[128] Also, Dijkgraaf had shown experimentally that bats could detect food as close as 5 cm away, which was seemingly too short a distance given the average wavelength of the bat's signal. Therefore Griffin supposed that the frequency drop probably facilitated close-range echolocation, since the waves at the beginning of the outgoing pulse would not overlap with the same frequency range of the returning echoes: "at close range the perception of any object by echolocation must involve discrimination between mixtures of original pulses and their returning echoes," and frequency sweeps would reduce the amount of noise generated by such overlaps in the bat's signal.[129] Thus Griffin applied the knowledge of acoustics and remote sensing that he had acquired during the war to bats, and in doing so he was able to gain a fuller understanding of echolocation. This new line of analysis was necessary to determine with greater precision just what kinds of information bats were able to acquire, in addition to the kinds of behaviors that could be based on echolocation. Further analysis of echolocation in bats would eventually lead Griffin into surprising new areas. To conclude this chapter, I will briefly highlight two of these, both of which show important connections to the military technologies of remote sensing: hunting and jamming.[130]

It is perhaps curious that it was not until 1950 that Griffin seriously pursued the question of whether bats hunted via echolocation. At least a decade before then he had read about Spallanzani's experiments on the auditory basis of bat orientation, which revealed that bats with plugged ears were incapable of filling their bellies with insects.

---

[128] Donald Griffin, "Measurements of the Ultrasonic Cries of Bats," p. 252. On radars and jamming, see: Mark Denny, *Blip, Ping, & Buzz*, p. 48-55.
[129] Donald Griffin, "Measurements of the Ultrasonic Cries of Bats," p. 252.
[130] There are other areas that also show salient connections, such as target discrimination and the use of echolocation in homing behavior. For the purposes of this chapter, I have limited my analysis to the two areas that seem most importantly connected.

Though hardly a smoking gun, those early accounts were at least suggestive that bats required their hearing for more than simply avoiding obstacles. But Griffin was a rigorous skeptic, and bats were not supposed to be capable of such complex behaviors. It was startling enough that they were capable of obstacle avoidance via auditory cues, and Griffin interpreted the results of his early experiments narrowly: obstacle avoidance was merely an automatic mechanism—a collision warning device. The metaphorical concept of echolocation, however, was a powerful key, capable of unlocking new doors that had previously been inaccessible or even invisible. The bat's ability to use echolocation in hunting insect prey was one such door.

In fact, Griffin came intriguingly close to entertaining that idea at least as early as 1941. In a letter to his colleague Charles Duckman, he suggested the possibility that bats used their acute sense of hearing to detect insects while hunting:

> I doubt if anyone knows exactly how they find the moths and flies and other insects which the [sic] catch on the wing. They may simply swoop about with their mouths open where the insects are very abundant, but I think they probably use sounds made by the insects as well. This is really just a guess on my part, but bats are so skillful at avoiding wires by means of the sound reflected back to them, that it would seem reasonable to suppose they might locate their food in the same fashion.[131]

This passage demonstrates how limited in scope Griffin conceived of obstacle avoidance at the time: the bat's sense of hearing was so sensitive for the purpose of obstacle avoidance that it could possibly leverage that sensitivity—*not to locate prey interactively via ultrasonic echoes*—but by simply hearing the insect's own sounds. At that time, of course, obstacle avoidance had not yet been generalized to echolocation, and thus Griffin had not begun to seriously consider the parallels between bats and radar.

---

[131] Donald Griffin to Charles Duckman, 22 February 1941, Series 1, Box 2, Folder [Corr – Di-Dy], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

A few years after the war, however, Griffin returned to the question of hunting, this time with a more expansive understanding of echolocation as a general method of perception. He would later explain that overlooking the possibility of hunting via echolocation was simply a failure of imagination earlier in his career: "Echolocation of stationary objects had seemed remarkable enough, but our scientific imaginations had simply failed to consider, even speculatively, this other possibility with such far-reaching ramifications."[132] As this chapter shows, Griffin's wartime experiences and the concomitant development of echolocation as a more generalized process went a long way toward expanding that imagination.

One crucial function of metaphor in science is to validate new kinds of questions by drawing separate domains together under the same conceptual framework. Griffin posed one such question to himself in 1951, wondering if bats used echolocation to hunt insect prey. He mused, "It is certainly reasonable to assume that they do, since their avoidance of small, inanimate objects is so clearly based on this natural analogy to radar or sonar instruments."[133] Griffin thus validated his biological speculation by drawing on its connections to the technological realm. The speculation, of course, was not without an evidentiary base.

As Griffin explained, the laboratory-based obstacle avoidance experiments were "not enough to bring this auditory mode of orientation into its complete biological perspective. For it does not reveal to what extent bats depend upon echolocation for their orientation under natural conditions, or how they locate and capture the flying insects that

---

[132] Donald Griffin, "Recollections of an Experimental Naturalist," p. 139.
[133] Donald Griffin, "At What Distance Can a Flying Bat Perceive Small Objects," *Journal of Mammalogy*, Vol. 32 (1951): 487.

form virtually their sole source of food."[134] The hunting research was partially funded through the Office of Naval Research, with whom Griffin would collaborate on several contracts in the years following the war. Evidently, some individuals in the ONR had an "active interest" in Griffin's analysis of bat echolocation.[135] Preliminary observations of bats in the wild, conducted with a portable setup of the ultrasonic detector, indeed showed that bats emitted their echolocation pulses while flying through caves and while hunting insects: "Bats thus appear *to search actively* for their insect prey by the same process of 'echolocation' previously demonstrated to be the basis of obstacle avoidance."[136] Although it was difficult to get consistent readings due to the highly directional nature of the bat's pulses (in the form of narrow beams), after a few months Griffin was able to obtain a substantial amount of data.

As a lifelong observer of bats, he knew that they engaged in two main aerial styles: the first he termed "cruising flight," which was relatively smooth and linear, and accompanied by the emission of a constant pulse rate. That style was punctuated by a second form, characterized by the sudden dives and twists necessary to capture flying insects. With a portable ultrasonic detector, Griffin found that the sounds that bats emitted during each flight pattern varied considerably. When bats changed from cruising to diving, their echolocation signals changed in three main ways: the length of each pulse shortened, the emission rate of pulses increased, and the degree of frequency modulation within each pulse also increased. After years of experience with remote sensing, both

---

[134] Donald Griffin, "Bat Sounds under Natural Conditions, with Evidence for Echolocation of Insect Prey," *Journal of Experimental Zoology*, Vol. 123, No. 3 (Aug 1953): 435-465.

[135] The ONR contract was construed broadly to investigate target discrimination in bat echolocation.

[136] Donald Griffin, "Acoustic Location of Insect Prey by Bats," *Anatomical Record*, Vol. 111, No. 3 (1951): 448-449. Emphasis mine. While *Myotis* was Griffin's perfect subject in the laboratory, he found that it was easier to record the sounds of *Eptesicus* when in the wild. Both species, however, showed the same patterns.

biological and technological, the reason for these acoustical changes was immediately obvious to Griffin: “in all cases the changes were of a sort that might be expected to give the bat more information about small objects at close range.”[137] This was indeed strong evidence that bats used echolocation for more than obstacle avoidance. As Griffin explained, on the basis of the acoustic changes alone he was “strongly inclined to conclude that these bats detect their insect prey by means of echolocation, and that they guide their pursuit on the basis of information perceived through multiple echoes from bursts of short duration.”[138]

Those strong inclinations notwithstanding, Griffin was a rigorous skeptic, and so he considered the possibility that bats might use another sense—not the echolocation method—to hunt. Olfaction was unlikely, since in addition to being ineffective at distances greater than one meter, bats also dove at pebbles and other objects that smelled nothing like insects. Similarly, vision was ruled out, since obstacle avoidance experiments had shown that bats were helpless flyers when forced to rely on sight alone. Given the extreme sensitivity of the bat’s ear, normal hearing was certainly possible, but the hunted insects’ sounds did not register to human ears or on the ultrasonic detector. Furthermore, Griffin reasoned that if bats relied on hearing insect sounds, then they probably would not emit such intense noises while hunting. Moreover, there was suggestive evidence that certain species of moths were capable of hearing sounds in the ultrasonic range, and consequently echolocation cries would alert those insects to the

[137] Donald Griffin, “Bat Sounds under Natural Conditions, with Evidence for Echolocation of Insect Prey,” p. 446.
[138] Donald Griffin, “Bat Sounds under Natural Conditions, with Evidence for Echolocation of Insect Prey,” p. 451.

presence of hungry bats.[139] A further reason to doubt the role of simple listening was due to "the eagerness with which they often pursued inert, artificial targets such as pebbles tossed gently into the air."[140] But what if bats captured pebbles simply by hearing the sounds produced by the projectiles as they cut through the air? To account for even this remote possibility, Griffin fashioned a blowgun from a piece of glass tubing and shot wads of wet cotton—"very silent missiles"—into the air. The bats were skilled at capturing these as well. All of this additional evidence and logical reasoning strongly suggested that echolocation was the primary method of capturing prey: "While many questions of detail remain unanswered, and more extensive quantitative studies of these phenomena remain desirable for the future, it seems clear that these bats employ the process of echolocation for more precise and complicated types of orientation than the mere avoidance of static obstacles."[141]

Although Galambos was not involved in these experiments, he wrote to Griffin upon learning the results, amusingly observing: "You are to be congratulated, again, and as usual, upon a very pretty piece of work. That train of 1 to 2 msec pips at a rate of 200 per sec is as beautiful a record of a scientific endeavor as I know. You ask the question, nature provides the bat and the pebble, and a good many thousands of Navy dollars gives us the answer. Science is so simple."[142] But science was not so simple, and Griffin would go on to explore hunting via echolocation in greater detail, expanding his studies to include several other species. He also moved these investigations back into the

---

[139] Donald Griffin, "Bat Sounds under Natural Conditions, with Evidence for Echolocation of Insect Prey," p. 452-453.
[140] Donald Griffin, "Bat Sounds under Natural Conditions, with Evidence for Echolocation of Insect Prey," p. 453.
[141] Donald Griffin, "Bat Sounds under Natural Conditions, with Evidence for Echolocation of Insect Prey," p. 455.
[142] Robert Galambos to Donald Griffin, 8 October 1951, Series 1, Box 4, Folder [Corr – Galambos], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

laboratory, where he was finally able to induce captive bats to hunt under artificial conditions. In experiments in the late-1950s he was joined by Frederic A. Webster, a psychologist and information theorist from the General Radio Company. These later experiments on hunting were better quantified than Griffin's previous work, and the team was able to obtain more accurate spectrographs of the echolocation cries.[143] The experiments strengthened Griffin's original findings, showing conclusively that echolocation was indeed the primary means by which these bats located, tracked, and captured insect prey.

Griffin incorporated these new findings into another popular essay comparing bats to radar and sonar.[144] "Thanks to sonar," he explained, "an insect-eating bat can get along perfectly well without eyesight." Close analysis of hunting bats had shown that their frequency modulations were actually correlated to the average size of insect prey: as the frequency swept downward, the wave-length of the pulse lengthened from 6 to 12 millimeters, which was the average size of their insect prey. Because the effective size of the insect changed as it maneuvered in the air, the frequency sweep thus helped the bat discriminate its moving targets. Griffin marveled, "the common impression is that it is merely a crude collision warning device. But the bats' use of their system to hunt insects shows that it must be very sharp and precise...All in all, we can say that bats obtain a fairly detailed acoustic 'picture' of their surroundings by means of echolocation."[145]

But by 1958 their ability to hunt insects was no longer what interested Griffin most about bats. The most impressive feature of echolocation, he explained, was the bat's

---

[143] Donald Griffin, Frederic A. Webster, and Charles R. Michael, "The Echolocation of Flying Insects by Bats," *Animal Behaviour*, Vol. 8 (1960): 141-154.
[144] Donald Griffin, "More about Bat 'Radar'," *Scientific American*, Vol. 199, No. 1 (1958): 40-44.
[145] Donald Griffin, "More about Bat 'Radar'," p. 42.

"ability to detect their targets in spite of loud 'noise' or jamming. They have a truly remarkable 'discriminator,' as a radio engineer would say."[146] The fact that bats so skillfully navigated caves in groups of hundreds or even thousands was a solid indicator that they possessed some kind of jamming avoidance ability. That is, the bat's signal was somehow not jammed by the hundreds of other bats nearby, all of which emitted signals at about the same frequency. Metaphorical reasoning once again validated the investigation of this problem, since electronic jamming was such a major focus in sonar and radar research during and after the war. Furthermore, the incorporation of information theory into communications research in the 1950s had led to a major focus on problems of discriminating signal information from noise. Griffin once again appealed to the bat's evolved system as a possible source of inspiration: perhaps those information theorists could "learn something from the bats, which have solved the problem with surprising success."[147]

Griffin had first begun to test the bat's susceptibility to jamming in experiments in the mid-1950s, thanks once again to an ONR contract.[148] With his graduate student Alan D. Grinnell, he set up an obstacle avoidance array inside a small room in Harvard's biology laboratories. In experiments similar to those that Griffin and Galambos had carried out, they quantified the ability of bats to avoid wires in different noise conditions.[149] Filling the room with "white" noise at 80-90 decibels—tuned to the same frequency of the bat's echolocation signal—slightly increased the minimum size of wires that they could detect. Nevertheless, the bats avoided the wires between 80% and 90% of

[146] Donald Griffin, "More about Bat 'Radar'," p. 42.
[147] Donald Griffin, "More about Bat 'Radar'," p. 44.
[148] Griffin developed a close working relationship with Sidney Galler, head of the biology branch at ONR.
[149] Griffin used *Plecotus* bats for these experiments.

the time, which was right at the average levels of avoidance in control conditions. Griffin and Grinnell concluded that the frequency sweep and the temporal delay between the emission of their pulses and the reception of those echoes probably prevented the bat signals from being jammed, but it would remain a problem for several decades. They would go on to study the problem of signal discrimination in the following years, in addition to researching the bat's target discrimination of different kinds of objects.[150] All the while Griffin hoped that knowledge generated by bat research would feed back into more general technological and scientific problems: "When I watch bats…employing their gift of echolocation in a vast variety of ways, I cannot escape the conviction that new and enlightening surprises still wait upon the appropriate experiments. It would be wise to learn as much as we possibly can from the long and successful experience of these little animals with problems so closely analogous to those that rightly command the urgent attention of physicists and engineers."[151]

Conclusion

Griffin's wartime experiences at Harvard profoundly shaped the way he approached the study of bats. As he later explained, by 1950 "whatever influences molded my scientific work and thinking had done their work," for he had "come to realize that bat echolocation was a highly versatile mode of perception."[152] The military technologies of communications signal processing and remote sensing constitute an important factor in effecting that change. During the war these factors facilitated the

[150] Donald Griffin, J.J.G. McCue, and Alan D. Grinnell, "The Resistance of Bats to Jamming," *Journal of Experimental Zoology*, Vol. 152, No. 3 (1963): 229-250; Alan D. Grinnell and Donald Griffin, "The Sensitivity of Echolocation in Bats," *Biological Bulletin*, Vol. 114, No. 1 (Feb. 1958): 10-22.
[151] Donald Griffin, "More about Bat 'Radar'," p. 44.
[152] Donald Griffin, "Recollections of an Experimental Naturalist," p. 138.

transmutation of Griffin's understanding of bat orientation from a mechanistic conception of obstacle avoidance into an interactive and general mode of perception. For Griffin, the obstacle avoidance ability was construed primarily in terms of the mechanistic relationship between the acoustic signal and the navigational reaction of the bat in flight. Echolocation, however, was understood to be a general mode of perception, or sensory tool, applicable to a variety of behaviors. The expansion of this view would eventually play a crucial role in Griffin's later work on animal consciousness, but the breakdown of mechanistic conceptions of animals was an important first step in that direction.

Griffin's conceptualization of echolocation as fundamentally similar to military technologies was deeply important in his biological thought, as it validated new questions and ideas about bats and their behavior. Metaphorically, "echolocation" joined the biological and technological spheres, generating new insights by considering the separate phenomena as resting on unified principles. Throughout his career, Griffin would often return to the study of echolocation, which he considered to be an unending "magic well" of scientific knowledge and inspiration.[153]

That Griffin's scientific development was shaped by new wartime technologies cannot be doubted. Moreover, the mediated use of technologies that extend or sharpen the human senses—such as sophisticated communications equipment, military radar, and infrared night vision—may have led Griffin to new insights about the interplay of consciousness and sensory systems in regulating animal behavior. In working with these technologies, Griffin was led to imagine how animals might be aware of their own behavior while utilizing complex sensory systems to accomplish various tasks. Later

[153] Donald Griffin, "Return to the Magic Well: Echolocation Behavior of Bats and Responses of Insect Prey," *BioScience*, Vol. 51, No. 7 (Jul. 2001): 555-556.

chapters will explore these ideas in greater detail. In an autobiographical memoir, Griffin intriguingly hints at this idea. Several years after the war, he crudely assembled a digitally adapted radar in order to track migrating birds, obscured by the clouds, from an airplane. In recalling this experience, Griffin explained that while "operating this apparatus I felt I *was* a bat."[154]

[154] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 87. Emphasis in the original.

CHAPTER 4
The Trouble with Bird Migration

Introduction

This chapter focuses on another perplexing area of animal behavior that Griffin investigated using his experimental approach to sensory physiology: bird migration and orientation.[1] As was the case with Spallanzani's bats, the ability of birds to migrate hundreds or thousands of miles was a longstanding biological problem that had yet to be resolved by the mid-twentieth century. Advancements in electrophysiological techniques in the 1920s and 1930s yielded a deeper understanding of the sensory physiology of animals, and of the physical and chemical features of their environments that were mediated by those senses. But it took an experimental approach using whole organisms—both in the wild and in the laboratory—to fully understand complex behavioral phenomena such as bird migration. By 1940 there were perhaps a dozen biologists seriously working on the problem, and most of these—such as Gustav Kramer, Werner Rüppell and Erwin Stresemann—came from the German ethological tradition. In England, the ornithologists Geoffrey V.T. Matthews and William Homan Thorpe led the way. And in North America, Griffin's work was complemented by that of evolutionary biologist and ornithologist Ernst Mayr, Canadian ornithologist William Rowan, and physicist Henry L. Yeagley, who conducted classified work on pigeon homing for the Army Signal Corps. While much of this research was suspended during the war (aside

[1] Migration refers to the specific temporal and spatial movements that most birds perform during annual cycles. Orientation refers generally to the ability of birds to recognize where they are in relation to proximate or distant goals. Homing refers specifically to the ability of birds to return to destinations from which they have been displaced; in the context of the chapter, homing mainly refers to the ability of artificially displaced birds in homing experiments, which test the ability of birds to return to their nests or home lofts from unfamiliar territories. On the whole, these phenomena fall under the category of navigation, which generally refers to the ability of birds to make directional adjustments in flight in order to reach their destinations.

from Yeagley's), there was a resurgence of interest in the problem in the 1940s and 1950s, and during this period Griffin became an authoritative figure in the field.

In his doctoral research between 1938 and 1942, Griffin first approached the problem from within the mechanistic conception of animal behavior, which was thus in accordance with his concurrent work on obstacle avoidance in bats. This research extended the early-twentieth century experiments conducted by physiological psychologist Karl Lashley, and Lashley's mentor at Johns Hopkins University, John B. Watson. For Griffin, the mechanistic approach consisted in identifying and describing both the sensory physiology that undergirded the behavior, and the environmental cues that were mediated by the senses. His doctoral work initially overlapped his bat research chronologically and thematically, for both entailed experimental programs that isolated sensory channels in order to make sense of more general behavioral phenomena. Unlike his work on bats, however, Griffin's bird research did not yield satisfying and clear answers, for he was not able to explain from the mere analysis of sensory mechanisms how birds performed their impressive migratory feats. This led him to explain his results by developing an exploratory theory of orientation, which held that birds navigated by random searching until they came upon environmental cues that led them into familiar territory and oriented them homeward. The precise nature of these cues, and the mechanisms by which birds made sense of them, however, still eluded Griffin. The mechanistic approach, which would be so effective in leading to the discovery of ultrasonic bat navigation, failed to yield a similarly clear picture of bird migration.

The second part of the chapter concerns a controversial orientation theory that challenged Griffin's exploratory theory in the late 1940s. It was in 1947 that

Pennsylvania State College physicist Henry L. Yeagley (1899-1996) published his magnetic theory of orientation. While working with carrier pigeons for the Army Signal Corps during the war, Yeagley developed a speculative theory, which held that pigeons oriented themselves on a geophysical grid generated by the perception of terrestrial magnetism and the Coriolis effect. Yeagley's publication of the theory in 1947 caused much excitement within the small but vocal community of American and British ornithologists and ecologists, but almost immediately several major problems with the work led scientists to reject his ideas and to question the soundness of his methods. Griffin was central to this critical response, as he and his colleagues privately organized several public rejoinders in a collaborative effort to discredit Yeagley's work. In fact, by the time Griffin learned about Yeagley's theory in the late 1940s, he had become increasingly skeptical of explanations based on simple stimulus-response mechanisms such as magnetic orientation theories. For Griffin, homing and migration were complex behaviors that could not be reduced to simplistic, Loebian mechanisms such as the magnetic theory held. Yeagley's dubious methodology and conveniently simple explanation only deepened Griffin's skepticism about magnetic orientation, of which he remained wary for the rest of his career.

By focusing on Griffin's approach to the problem of homing and migration, this chapter demonstrates how experimental methods in sensory physiology were used to understand more general questions about animal behavior. While grappling with these phenomena, Griffin's mechanistic assumptions about the simplicity of animal behavior began to break down, as this framework was incapable of making sense of complex behavioral problems. Throughout his bird research in the 1940s, Griffin interpreted his data according to the simplest possible explanation: birds navigated using random exploration and the known senses, and until firm evidence indicated otherwise, he continued to opt for the conservative interpretation.[2] This hermeneutic proved useful in rejecting speculative or unwarranted theories such as Yeagley's. But where it limited speculation, it also limited imagination. As I analyze in the fifth chapter, migration research in the 1950s would show that birds possessed a biological clock, and that they were able to draw on it in order to navigate by calculating the motion of the sun and stars.

Griffin's approach to the problem of bird migration yielded useful data, but his interpretations were overly conservative, and obscured some of the essential features of bird behavior. In the 1950s he continued his investigation of migration and homing, and came to realize that birds were even more complex than he had previously imagined. Before that realization took place, however, he would have to simplify the problem by developing new methods such as airplane tracking in artificial homing experiments. This work, which began with his doctoral research and continued after the war, took place alongside Griffin's research on bats. Together, these investigations expanded Griffin's view of animal behavior, and would eventually play an important role in leading him to formulate new ideas about animal consciousness in the 1970s.

[2] Griffin would later describe this experimental philosophy as the application of "simplicity filters." Like Ockham's razor or "Morgan's canon," simplicity filters were intended to keep one's imagination in check, and to demand overwhelming evidence for new ideas or complex explanations of behavioral phenomena. In effect, this epistemology judges the quality of scientific explanations according to their conceptual simplicity.

The Trouble with Bird Migration

Upon completion of his B.S. in biology in 1938, Griffin had already decided to do his graduate work at Harvard, but he lacked a suitable research agenda. Further experiments on bats did not seem overly promising, since at that point he and G.W. Pierce had incorrectly concluded that ultrasonic sounds were not used for orientation. He strongly desired to research some topic in behavioral biology, but this apparently did not sit well with the physiologically oriented faculty at Harvard. Fortunately for him, Karl Lashley—a renowned physiological psychologist who was chiefly concerned with problems of animal behavior—had been jointly appointed to the psychology and biology departments in 1935.[3] Although Griffin had little interaction with him prior to 1938, Lashley nevertheless agreed to supervise his research on bird migration, a topic of mutual and longstanding interest. Griffin's decision to study birds was not a particularly curious one, for he had wondered since childhood how birds, bats, and other animals knew how to get from one place to another.[4] Studying bird migration was thus a logical choice, but apparently not a popular one. Griffin later recalled, "Bird navigation had begun to fascinate me, but wiser heads emphasized that if I really wanted to be a serious scientist I should put aside such childish interests and turn to some important subject such as

---

[3] The psychology department had only recently split from philosophy (1934) as part of Harvard president James Conant's university-wide academic reforms. Conant pushed hard to improve the psychology department's reputation by seeking out several distinguished experimentalists, and landing the esteemed Karl Lashley was a major coup. See Morton Keller and Phyllis Keller, *Making Harvard Modern: The Rise of America's University* (Oxford: Oxford University Press, 2001), p. 89-90. On Karl Lashley's physiological psychology, see Nadine Weidman, *Constructing Scientific Psychology: Karl Lashley's Mind-Brain Debates* (Cambridge: Cambridge University Press, 1999).

[4] As an undergraduate, he extended those amateurish interests into formal studies on the annual migratory patterns of bats from winter caves to summer roosts in New England: Donald Griffin, "Marking Bats," *Journal of Mammalogy*, Vol. 15, No. 3 (Aug. 1934): 202-207; Donald Griffin, "Bat Banding," *Journal of Mammalogy*, Vol. 17, No. 3 (Aug. 1936): 235-239; Donald Griffin, "Bat Banding: A Request for Cooperation," *The Auk*, Vol. 53, No. 2 (Apr. 1936): 253-254; Donald Griffin, "Wings without Feathers," *New England Naturalist*, Vol. 3 (Sep. 1939): 11-13; Donald Griffin, "Bats Migrate Too," *New England Naturalist*, Vol. 5 (Dec. 1939): 1-4.

physiology."[5] Nevertheless, he ignored his elders' concerns and pushed forward with his doctoral plan. In order to investigate the problem, Griffin extended an experimental program conducted in the early-twentieth century by Lashley and John B. Watson.

Watson worked on bird migration between 1907 and 1913, during which time he joined and later became chair of the psychology department at Johns Hopkins University.[6] He conducted his first experiments on Bird Key in the Dry Tortugas, about eighty miles west of Key West in the Gulf of Mexico.[7] At that point he had not yet articulated the brand of arch-behaviorism that would come to define his legacy in American psychology, although his work on bird behavior was certainly not mentalistic.[8] Bird migration is an inherently difficult topic to study, since the spatial and temporal dimensions of migrations are typically so vast that no individual observer can witness a single course in its entirety. Watson assumed that birds navigated toward proximate goals simply using their keen sense of vision, but distant orientation—toward unseen goals, as in the case of long migrations—was more problematic.

---

[5] Donald Griffin, "Recollections of an Experimental Naturalist," in *Leaders in the Study of Animal Behavior*, ed. Donald Dewsbury, p. 120-142 (Cranbury, NJ: Associated Universities Press, 1985), p. 127.

[6] Watson joined the psychology faculty at Johns Hopkins in the fall of 1908. Shortly thereafter, chair James Mark Baldwin became embroiled in an infamous prostitution scandal, and was forced out of the university. Watson subsequently became chair in 1909.

[7] This and future work was funded by the Carnegie Institute of Washington, which had established an outpost of the Marine Biological Laboratory on Bird Key. John Watson, "The Behavior of Noddy and Sooty Terns," *Papers from the Department of Marine Biology, Carnegie Institution of Washington* [Tortugas Laboratory Papers], Vol. 2, No. 103 (1908): 187-255; John Watson and Karl Lashley, "Homing and Related Activities of Birds," *Papers from the Department of Marine Biology, Carnegie Institution of Washington* [Tortugas Laboratory Papers], Vol. 7, No. 211 (1915): 1-104; John Watson, "How Animals Find Their Way Home," *Harper's Monthly Magazine*, Vol. 119 (Oct. 1909): 685-689.

[8] On Watson's life and work, see Kerry W. Buckley, *Mechanical Man: John B. Watson and the Beginnings of Behaviorism* (New York: The Guilford Press, 1989). On Lashley's work with Watson, see: Nadine Weidman, *Constructing Scientific Psychology*, p. 32-47.

At the time, most theories that attempted to account for this ability were speculative, and often involved positing a special "sixth sense."[9] For example, the nineteenth-century French zoologist Camille Viguier (1850-1930) proposed a theory in 1882, claiming that pigeons possessed a refined sense of terrestrial magnetism that enabled them to orient their long-distance flights.[10] Gabriel Reynaud, an officer in the French Army's homing pigeon service, similarly offered his "contrepied theory" of navigation, which held that when pigeons returned from great distances, they merely backtracked by retracing the steps of their outbound route.[11] Also noteworthy was amateur naturalist Pierre Hachet-Souplet's (1867-1947) visual landmark theory, which held that distant orientation was different from proximate orientation only in degree, not in kind.[12] In short, he suggested that birds relied on a series of familiar visual landmarks to navigate, merely increasing their altitude in order to see more distant landmarks. Other theorists turned to the vague and protean concept of instinct, shrugging their shoulders and concluding that birds simply possessed a "homing instinct" that required no further explanation.

Watson, however, was unconvinced. Viguier's magnetic theory and Reynaud's contrepied theory were too speculative, unsupported as they were by convincing experimental evidence. Furthermore, they were centered on the homing pigeon, a domesticated species that required careful breeding and intensive training in order to

---

[9] The five "Aristotelian senses" being vision, hearing, touch, olfaction, and taste. The invocation of a "sixth sense" is reminiscent of early-modern explanations of bat orientation by some mysterious ability.
[10] Camille Viguier, "Le sens de l'orientation et ses organes chez les animaux et chez l'homme," *Revue Philosophique de la France et de l'Etranger*, Vol. 14 (1882): 1-36. Aside from a few publications, there is very little record of Viguier or his work.
[11] Gabriel Reynaud, "The Orientation of Birds" [Translated], *Bird Lore*, Vol. 2, No. 4 (Aug. 1900): 101-108.
[12] Pierre Hachet-Souplet, "Quelques experiences nouvelles sur les pigeons voyageurs," *6th Congrès International de Psychologie* (1909): 663-673.

achieve such feats of navigation. Hachet-Souplet's visual landmark theory was more credible, but it could not account for homing across vast distances where no landmarks were visible, such as journeys on the open ocean. A simple calculation revealed that due to the curvature of the earth, birds would have to fly to unattainable heights in order to see distant landmarks.

To simplify the problem of studying migration, Watson designed a series of artificial homing experiments using two species of oceanic birds, noddy and sooty terns (*Anous stolidus* and *Onychoprion fuscatus*, respectively). Successful experiments would require a comprehensive understanding of the birds and their way of life, and so Watson spent May and June of 1907 in the Dry Tortugas meticulously studying the birds' nesting and feeding "instincts."[13] In the early-twentieth century, the protean concept of instinct had become rather capacious after several decades of post-Darwinian biology and psychology. To some it meant the set of behaviors displayed by a particular species, and thus it was used phylogenetically. In the naturalist and British comparative psychology traditions, it typically meant those innate behaviors that animals were capable of exhibiting without learning. And for Watson, as for Jacques Loeb and other reductionist physiologists, it signified behavior that was seemingly impulsive or automatic, triggered by some external—or perhaps internal—stimulus.[14]

Watson's experiments, first conducted in 1907 on Bird Key, entailed removing birds from their nests and shipping them in covered crates to increasingly greater

[13] In studying the impulsivity of the terns' feeding instinct, for example, Watson found that they ate only live minnows that skipped above the water.
[14] On the meanings of instinct, see: Robert Boakes, *From Darwin to Behaviourism: Psychology and the Minds of Animals* (Cambridge: Cambridge University Press, 1984), p. 204-206.

distances in order to measure their ability to return home from unfamiliar territory.[15] Noddies and sooties were ideal experimental subjects for several reasons. For one, they spent most of the year along the shores of the Caribbean islands, gathering each May by the tens of thousands on Bird Key to mate, socialize, and rear offspring. Thus they existed in large numbers, and had the added benefit of being relatively easy to catch. Also, Bird Key lies at the northernmost point of their natural range. This meant that all of the territory north of the Tortugas was almost certainly unfamiliar to the birds—an ideal condition for homing experiments. Finally, they were strongly incentivized during brooding season to return as quickly as possible to their nests in order to protect their offspring; homing experiments could thus take advantage of this instinct. One potential setback, however, was their refusal to eat anything other than live minnows, to which they were instinctually adapted. Keeping the birds healthy in captivity was thus a difficult task and resulted in several failed experiments wherein birds died or could not fly due to their deteriorated condition.[16]

Toward the end of his time on Bird Key, after weeks of painstaking work in the heat, Watson carried out his initial homing experiments. He first sent pairs of birds into territory that was assumed to be familiar to them (to the east and south of Bird Key). These birds had no trouble returning from distances of 20, 44, 66, and 108 miles, although their slow return times suggested that they did not fly home directly. Homing

[15] The crates were covered with canvass so that the birds could not see any details of the external environment.

[16] John Watson, "How Animals Find their Way Home," *Harpers Monthly Magazine,* Vol. 119, No. 713 (Oct. 1909): 685-689; John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 35-38.

from familiar territory, therefore, seemed relatively unproblematic. The crucial question was how they would fare in unfamiliar territory.[17]

Since brooding season was coming to an end in mid-June, Watson was only able to conduct one of these critical experiments before he had return to Hopkins. He arranged to have five birds (two sooties and three noddies) shipped far up the Atlantic coast to a release point off the shore of North Carolina. A caretaker escorted the birds on their 72-hour journey into unfamiliar territory near Cape Hatteras, approximately 850 miles northeast of Bird Key. Watson carefully observed their nests for the next several days until amazingly, three of the five returned to their nests.[18] He assumed that due to their feeding and flying habits, which necessitated that they remain near the shore, the birds had followed the Atlantic coast south and rounded the southern tip of Florida, rather than flying directly overland. From the results Watson concluded, "there can be no doubt that my birds were carried into a wholly unknown territory, and since they returned, the question as to how they did it is the one which it is hoped future experiment will answer…It seems to me that the 'visual landmark' theory of distant orientation is forever exploded by these tests. What we shall put in place of it is difficult to decide."[19]

Watson took the next steps in these investigations when he returned to Bird Key in the summer of 1910, arranging additional releases from New York harbor, Galveston (Texas), and Mobile (Alabama).[20] These experiments, however, were mostly disastrous. The twelve birds sent to New York were weakened due to shipping delays that extended their captivity; none were ever seen back in the Tortugas. Along the Galveston route,

---

[17] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 46-47.
[18] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 46-47. Both the sooties returned on the fifth day, and one noddy returned several days after that.
[19] John Watson, "How Animals Find Their Way Home," p. 688.
[20] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 47-52.

eight birds (four noddies and four sooties) were released in May of 1910 from a point approximately 461 miles northwest of Bird Key.[21] One died en route, and only two of the remaining seven apparently made it back to their nests. Of the thirteen noddies and sooties slated for release in Galveston harbor, two died en route, and the rest never made it back. The results were even worse in the Mobile group: none of the fourteen birds returned to Bird Key.[22] Despite these seemingly negative results, Watson maintained that homing from unfamiliar territory was still possible. However, he realized that the experiments required much healthier birds than he was able to maintain for the extended trips. A few years later he would try again, hoping to solve the puzzle of bird migration once and for all.

Watson had much better luck in the summer of 1913 when Karl Lashley, a graduate student in psychology at Hopkins, joined him on Bird Key.[23] Lashley proved to be excellent in the field, conducting important research on the visual sense of birds, particularly when it came to nest recognition and proximate orientation. He found that the bird's ability to locate its nest was much more complex than he or Watson had previously suspected, as the relationship between the visual stimulus and the behavioral response was more intricate than a simple one-to-one mechanism. If proximate orientation were thus more complex than the bird simply seeing its nest and flying toward it, how much more complex must distant orientation be, Lashley supposed. In addition, he was a meticulous observer and caretaker, and he became adept at monitoring and maintaining

[21] Noddies and sooties must be fed live minnows in order to keep them healthy in captivity. This caused occasional difficulties, particularly with a group that was released in New York harbor, already in a weakened state. Watson estimated that the weak birds would have had to travel 1000 miles in order to find live minnows, which explained why none returned to Bird Key.
[22] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 47-52.
[23] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 52-58. Lashley's doctoral advisor was zoologist and geneticist Herbert Spencer Jennings, but he also worked extensively with Watson during his time at Hopkins.

the birds' health during the captivity required by homing experiments. Thus with Lashley's aid, Watson was finally able to conduct successful experiments.[24]

Their work yielded exciting, though inconclusive, results. In May of 1913, Lashley escorted twenty-four terns aboard a steamship bound for Galveston.[25] Although he had to force-feed several of the birds in order to keep them properly nourished, most were released in fair condition. From the nearest release point, 418 miles northwest of Bird Key, two terns never returned. However, eight of ten birds successfully returned from a point 585 miles away; two birds released from 720 miles both returned; and three of ten released from 855 miles away returned. All told, slightly more than half of the twenty-four birds found their way home from unfamiliar territory.[26] Although the homing performance was not perfect, it was significant enough to convince both Watson and Lashley that these birds did possess a definite homing ability, despite the absence of visual landmarks. They interpreted their results as follows: "Our contributions are admitted to be negative in character. The difficulty of explaining homing by current theories is seen to be great, but, while admitting this, we do not suggest the assumption of some new and mysterious sense. The task of explaining distant orientation is an experimental one, which must yield positive results as soon as proper methods are at hand."[27] Future work, they concluded, should extend homing experiments to additional bird species and in greater numbers, paying particular attention to controlling aspects of the birds' sensory physiology.

---

[24] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 52-58.
[25] A few weeks prior, Lashley oversaw a disastrous trip to Mobile, where shipping delays, storms, and the inability to find live minnows resulted in yet another set of unhealthy homing subjects. He learned quickly how to better care for the birds, and future experiments were more favorable.
[26] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 54-58.
[27] John Watson and Karl Lashley, "Homing and Related Activities of Birds," p. 60.

Lashley's work on proximate orientation had also revealed an important clue. According to his experiments on nesting terns, the visual mechanism that led birds to their individual nests consisted in a type of pattern recognition, wherein birds noticed certain spatial relationships between their nests and other conspicuous objects in the surrounding areas.[28] Experiments showed that replacing a bird's nest with an artificial one, for example, did not hinder its ability to locate the nest. However, moving their nests sideways merely a few inches confused the birds, rendering them unable to locate them. Lashley assumed that this resulted from the bird perceiving more holistic visual qualities of the objects surrounding their nests (which included hundreds of other nests in the immediate area).

Lashley also found, however, that navigation to the nest was machinelike, as it entailed a set of coordinated, muscular movements, which he termed kinaesthetic habits. Birds did not simply fly directly to their nests upon seeing them; rather, they performed a ritualistic approach, which could be disrupted by the slightest rearranging of aspects of the visual environment. They first flew to a specific "alighting place," which was within visual range of and oriented them toward their individual nests. Next, "after orientation is gained the path to the nest is determined largely by motor habits irrespective of the immediate visual stimuli."[29] Thus the slightest change to the arrangements of objects surrounding the nest would lead the bird to forego this ritual, and it would instead fly off from the alighting place with no apparent knowledge of the nest's location.[30] Further

---

[28] Karl Lashley, "Homing and Related Activities of Birds [Notes on the Nesting Activities of the Noddy and Sooty Terns]," p. 61-83.
[29] Karl Lashley, "Homing and Related Activities of Birds [Notes on the Nesting Activities of the Noddy and Sooty Terns]," p. 72.
[30] A confused bird, whose nest area had been altered in some important way, would often return to the alighting place after its failure to locate the nest. Lashley thought that this was a process of "re-orientation."

work on the recognition of the young solidified Lashley's view that the nature of visual stimuli and memory in birds was intricate. Recognition of the young, like nest localization, was also "the result of a complex of many sensory-motor reactions, not merely of a single type of stimulus."[31]

This discovery had an important influence on Lashley's future psychological work.[32] Despite the behaviorist trajectory that Watson took shortly after their work in the Tortugas, Lashley in his career maintained a broader view of psychology, incorporating behaviorist methodologies alongside theoretical insights from schools such as the German gestalt psychologists.[33] For a brief time, his work with Watson on the conditioned reflex in 1915 convinced Lashley that behavioristic approaches were the best path forward in an objective psychology. In the 1920s, however, Lashley began to distance himself from behaviorism, while nevertheless maintaining that the properties of mind could be reduced to its physical components.[34] He thus remained committed to a physiological view of psychology, which attempted to correlate the physical and

[31] Karl Lashley, "Homing and Related Activities of Birds [Notes on the Nesting Activities of the Noddy and Sooty Terns]," p. 79.
[32] In her social constructivist interpretation of Lashley and his career, historian Nadine Weidman focuses mainly on Lashley's role in debates about hereditarianism. Although she does not analyze his work on bird navigation, my analysis of Lashley's definition of instinct is consistent with Weidman's view that Lashley struggled to find a middle ground between reductionism and holism in his consideration of animal behavior and instinct.
[33] In an address to Columbia University in 1913, Watson delivered his famous "behaviorist manifesto," in which he argued that the subject of psychology was behavior, not consciousness or minds, and that the proper experimental method was the analysis of external, quantifiable behavior within a stimulus-response framework. The goal of psychology, he explained, was the prediction and control of behavior, and subjective concepts such as consciousness, along with unreliable methods such as introspection and anecdotalism, ought to be forever banished from the science. John Watson, "Psychology as the Behaviorist Views It," *Psychological Review*, Vol. 20, No. 2 (Mar. 1913): 158-177. On Watson's life, career, and the origins of behaviorism, see Kerry W. Buckley, *Mechanical Man: John Broadus Watson and the Beginnings of Behaviorism* (New York: The Guilford Press, 1989), especially p. 73-111.
[34] Nadine Weidman, *Constructing Scientific Psychology*, p. 44-46. See also: Karl Lashley, "The Behavioristic Interpretation of Consciousness II," *The Psychological Review*, Vol. 30, No. 5 (Sep. 1923): 329-353.

chemical mechanisms in the brain with more general behavioral phenomena.[35] And whereas Watson would reject the very concept of consciousness, which was seemingly impossible to study in an objective fashion, Lashley instead came to see consciousness as a viable concept that was amenable to investigation in terms of the physical process of the brain.[36]

Thus while Watson and Lashley could not provide a comprehensive explanation of bird migration, their collaborative work did clarify many of the problems that it entailed. By successfully executing homing experiments, they were able to show that birds could indeed return from unfamiliar territory, despite the fact that they were unable to explain how these feats were accomplished physiologically. Furthermore, their experiments could serve as a model for future investigations, as in the case of Griffin's later work. And for Lashley especially, the research served as a foray into both methodological and conceptual problems in the physiological analysis of animal behavior. It also challenged him to think seriously about the problem of instinct; in future work, Lashley would attempt to remove some of the confusion surrounding animal behavior by investigating the physiology of sensory mechanisms, which for him were more precise categories of analysis than broad concepts such as instinct. His work with Griffin should similarly be viewed as part of Lashley's general effort to explain complex behavioral phenomena by identifying specific sensory mechanisms that undergird those patterns of behavior. By the time Lashley was called upon to advise Griffin's doctoral work in 1938, several decades of research in other areas of psychology had prevented

---

[35] As Nadine Weidman has argued, Lashley's balancing of external behavior with inner nervous processes reflected the dual focuses of his two advisors, Herbert Spencer Jennings (internal) and John Watson (external). Nadine Weidman, *Constructing Scientific Psychology*, p. 23-47.

[36] Karl Lashley, "Persistent Problems in the Evolution of Mind," *The Quarterly Review of Biology*, Vol. 24, No. 1 (Mar. 1949): 28-42.

him from returning to the problem of bird navigation, but his ideas about the complex nature of visual stimuli made themselves known in Griffin's work.

Griffin's Work on Bird Navigation

Despite Watson's and Lashley's success in experimentally defining the problem of homing by 1913, over the next twenty-five years little progress was made beyond that initial work. As evolutionary biologist and ornithologist Ernst Mayr explained in 1937, bird migration and homing remained "one of the greatest unsolved puzzles of modern biology."[37] In Mayr's view, the three most likely physiological explanations were vision, kinaesthesia (or "retracing"), and magnetic sensitivity (the same three possibilities specified by Watson in his 1913 assessment). Each theory was problematic in its own way, especially the magnetic and retracing theories, since birds did not seem to possess organs sensitive to magnetism, and the retracing theory required a kinaesthetic memory that was much more precise than that which birds seemed to possess.[38] Mayr in fact could point to only a few significant advances in the experimental analysis of homing since Watson and Lashley. An exception was German ornithologist Werner Rüppell's work on starlings and swallows, which Mayr cited as the most important homing research in the previous twenty-five years.[39] Similarly, Scottish ornithologist Arthur Landsborough Thomson's (1890-1977) contemporary survey of migration studies listed only a handful

[37] Ernst Mayr, "The Homing of Birds," *Bird-Lore*, Vol. 39 (Jan.-Feb. 1937): 5-13.
[38] Ernst Mayr, "The Homing of Birds," p. 10-11.
[39] Werner Rüppell, "Heimfindeversuche mit Staren 1934," *Journal für Ornithologie*, Vol. 83, No. 3 (1935): 462-524; Werner Rüppell, "Heimfindeversuche mit Staren und Schwalben 1935," *Journal für Ornithologie*, Vol. 84, No. 2 (1936): 180-198; Werner Rüppell, "Heimfindeversuche mit Staren, Rauchschwalben, Wendehälsen, Rotrückenwürgern und Habichten [1936]," *Journal für Ornithologie*, Vol. 85, No. 1 (1937): 120-135.

of significant attempts to solve the problem of homing.[40] Among the more important developments, according to Thomson, was Canadian ornithologist William Rowan's work on seasonal directionality and induced migratory behavior.[41] And like Mayr, Thomson identified Rüppell's homing work as particularly important, despite the fact that his efforts had not led to a full resolution of the problem.[42]

Rüppell's experiments in the mid-1930s showed that starlings and swallows had a definite homing ability, but his results were difficult to explain using a visual theory of orientation because of the relationship between the distance of displacements and the speed of the birds' returns.[43] The visual exploration theory necessitated that the amount of unfamiliar territory that birds would have to explore should increase according to the square of the distance between the release points and their home nests: tripling the straight-line distance, for example, would increase the area of unfamiliar territory by a factor of nine. Thus if one assumed that birds flew at relatively constant speeds while exploring unfamiliar territory, then the time it should take them to return should increase exponentially as well. Rüppell's data showed, however, that the return time increased arithmetically.[44] The results seemed to imply that birds possessed some other mechanism than visual exploration that provided them with a sense of the home direction or location:

---

[40] A. Landsborough Thomson, "Recent Progress in the Study of Bird-Migration: A Review of the Literature, 1926-1935," *Ibis*, Vol. 27 (1936): 472-530. Most of Thomson's review concerns the general studies of migration that apparently flourished during the 1920s and 1930s, particularly in Germany. These, however, mainly concerned features other than homing or the mechanism of orientation, such as migration routes, seasonal periodicity, comparative studies of migratory species, and more general behavioral characteristics of migratory birds. In a brief section on homing research, Thomson additionally cites the work of a few other zoologists as well, but Rüppell's was the most extensive.
[41] A. Landsborough Thomson, "Recent Progress in Bird-Migration," p. 506-508.
[42] A. Landsborough Thomson, "Recent Progress in Bird-Migration," p. 516-517.
[43] Werner Rüppell, "Heimfindeversuche mit Staren, Rauchschwalben, Wendehälsen, Rotrückenwürgern und Habichten [1936]," *Journal für Ornithologie*, Vol. 85, No. 1 (1937): 120-135.
[44] Mayr, "The Homing of Birds," p. 10-11.

“eine Sinnes-Empfindung für die Lage der Heimat,” according to Rüppell.[45] He therefore concluded that more experimental work on the physiology of homing (“Heimfindeversuche”) was thus necessary to determine the precise nature of the sense of direction that enabled birds to navigate from unfamiliar territory.

Thus when Griffin approached the problem in 1938, there were several suggestive lines of inquiry about the mechanism of homing, but few definite answers. And although he retrospectively characterized his decision to take up the problem of migration as an unpopular one within Harvard’s biology department, it was clearly a promising and legitimate research question with which other scientists were grappling. Biologists such as Mayr clearly saw value in taking up the problem: “The study of homing is a promising field for the enthusiastic bird student.”[46] And so with Lashley as his advisor, Griffin began working on the problem of migration and homing as a graduate student in the spring of 1938.

Like Rüppell and Mayr, Griffin was primarily interested in the natural behavior of birds—migrations in particular—but he took Watson’s and Lashley’s lead in using artificial homing experiments as a way to simplify the problem. His approach was strictly confined to questions of sensory physiology: ignoring the problematic concept of “instinct,” he focused on the sensory mechanisms and environmental cues that were necessary for homing.[47] Griffin’s initial experiments with Leach’s petrels took place in the summer of 1938 off the shore of the Bowdoin Scientific Station on Kent’s Island

---

[45] Werner Rüppell, “Heimfindeversuche mit Staren, Rauchschwalben, Wendehälsen, Rotrückenwürgern und Habichten [1936],” p. 135.
[46] Ernst Mayr, “The Homing of Birds,” p. 5.
[47] He did of course have to pay attention to specific aspects of behavior in order to conduct the experiments. For example, if petrels are removed from their nests before eggs are laid, they will almost certainly not attempt to return. It is therefore crucial to capture them during brooding season, which for the petrels of Kent’s Island, is in early July.

(New Brunswick). Enlisting the help of cargo ship crews to release banded birds at different distances and locations offshore, he assessed homing performance by two metrics: speed and percent of returns to the nest.

Griffin's work between June and August of 1938 consisted of five distinct experiments, most of which utilized several different experimental groups along with controls.[48] Because sensory mechanisms were his primary focus, he designed variations in the experimental conditions and handling of birds in order to isolate the senses used in homing. For example, in his third experiment he designed tests for two popular, yet unconfirmed, theories of distant homing: magnetism and the kinaesthetic sense, or directional memory. Twenty birds were released 280 miles from their nests after being rotated in their cages atop a phonograph on the outward journey. The rotations were intended to disrupt the mechanical sensations of the bird's inner ear labyrinth, which was thought to play an important role in directional memory. A second experimental group of twenty birds was exposed to a powerful electromagnet before being released. This, Griffin supposed, ought to reveal whether the bird's ability to sense magnetism played a role in homing. A control group of twenty untreated birds was released at the same time, and Griffin found that neither the phonograph nor the electromagnet had a significant impact on the return rates of the birds. In fact, the magnetized birds curiously found their way home slightly faster. He could offer no explanation for this result, although the difference was not statistically significant.[49]

Apparently vision was not a significant factor in homing either, as the return rates for birds displaced out of range of visual landmarks did not vary significantly from the

[48] Donald Griffin, "Homing Experiments with Leach's Petrels," *The Auk*, Vol. 57, No. 1 (Jan. 1940): 61-74.
[49] Donald Griffin, "Homing Experiments with Leach's Petrels," p. 63-71.

rates of birds that were released within sight of the shore. In fact, in nearly all of his experiments, at least fifty percent of the birds eventually found their way home. Furthermore, birds released from more distant points homed about as fast as those released closer to their nests. This seemed to indicate that birds did not wander randomly home, since more distant releases should require exponentially larger areas of unfamiliar territory that the birds would have to explore.[50] What explained the ability to home from unfamiliar territory? Essentially, these initial investigations left Griffin perplexed. However, the experience taught him how to design, execute, and evaluate future homing experiments. And the fact that his initial results were inconclusive indicated that it would be a worthwhile subject for his doctoral thesis.

The bulk of that doctoral work took place during the following summers between 1939 and 1941. With Lashley's guidance, Griffin conducted additional homing experiments using common terns and herring gulls on Penikese Island in Buzzard's Bay (Massachusetts).[51] Over the course of these investigations, birds were shipped as far away as Chicago and Savannah, constituting the largest displacements that he tested. Griffin also realized that in order to secure any firm knowledge about homing, he would have to track the birds as they attempted to return from unfamiliar territory. Only by direct observation, he reasoned, could one solve the problem of homing, and he therefore arranged to follow birds by airplane for several experiments.[52] He was evidently quite inspired by the airplane observations, explaining that "there is an indefinable feeling in

---

[50] Donald Griffin, "Homing Experiments with Leach's Petrels," p. 72-73.
[51] Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," *Bird-Banding*, Vol. 14, No. 1/2 (Jan-Apr. 1943): 7-33. Griffin's research was supported by a private donor, the Harvard Society of Fellows, Woods Hole, and Harvard physiologist Alexander Forbes, a professor in the medical school. The article was based on parts of his doctoral thesis.
[52] He was only able to follow a few homing flights, but several years later he expanded this method of studying homing. He also purchased a small aircraft, which he learned to pilot.

watching a bird from the air that one is in the bird's own medium and can understand its problems and behavior far better than would ever be possible from the ground."[53]

Over the course of three consecutive summers, 176 herring gulls were released at distances ranging from 15 to 872 miles: 93% returned successfully. Griffin found that gulls were generally successful at homing from both familiar and unfamiliar territory.[54] In familiar territory, 100% returned from distances up to 300 miles, and 80% returned from 870 miles.[55] From unfamiliar territory, the gulls were still fairly successful, although they homed better from coastal, as opposed to inland, release points: from releases in unknown coastal territory, 100% returned from 300 miles, and 87% returned from distances up to 445 miles. From unknown inland territory, 92% returned from distances up to 300 miles, 60% returned from 540 miles, and 67% retuned from 870 miles away. Thus Griffin found that gulls could home very well from both familiar and unfamiliar territory, although releasing them in unfamiliar inland territory negatively affected their homing. The fact that the nature of the territory affected the gulls' ability to return was a curious finding, and Griffin would attempt to make sense of this problem in future experiments.

The terns did not fare as well: 42.5% of the 80 birds definitely returned to their nests from distances between 94 and 404 miles away. Of those released in known territory, 100% returned from 102 miles away, 60% returned from 234 miles away, and 56% returned from 404 miles away.[56] The results were notably worse when terns were

[53] Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 12.
[54] Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 13-30. The layout of Griffin's data charts is particularly unclear, although it is possible to make sense of the average return data on page 19 by cross-referencing it with specific information on pages 13-15 and pages 27-30.
[55] Griffin did not provide specific numbers for the birds used in these releases.
[56] The total percent of returns was 68.4% (13 of 19 birds in total).

released into unfamiliar territory: 80% returned from 90 miles away, 30% returned from about 230 miles away, 24% returned from about 400 miles away. Unlike the gulls, the terns' homing was starkly better in familiar versus unfamiliar territory, and the percent of returns consistently decreased as they were released farther into unfamiliar territory. Their homing ability, however, was not affected by inland versus coastal releases in unfamiliar territory. Griffin concluded that terns' relatively poor homing performance was probably due to several factors, including the fact that gulls preferred soaring to flapping, and could therefore conserve energy while riding thermal updrafts. In addition, the feeding habits of terns were more specialized than gulls. This may have led them to become more inclined to explore local territory for the purpose of finding food, at the expense of their ability to home from unfamiliar territory where food was scarcer.[57]

In general, the speed of returns varied greatly in his experiments, indicating that nearly all birds either deviated from a straight course or took long breaks during flight. Very few birds returned home from either familiar or unfamiliar territory at speeds even approaching their known velocities. Birds released close to home, in fact, returned more slowly relative to those shipped farther away. Griffin wondered if this meant that orientation required a minimum amount of time that was relatively constant and independent of distance. However, three herring gulls did show "marked improvement" in their speeds when they were released from the same location a second time (in 1940 and 1941).[58] This indicated that the birds had probably become familiar with at least some aspect of the formerly unfamiliar territory, or had in some way become more adept at homing, although Griffin could not say which. In addition, gulls that were released in

---

[57] Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 20.
[58] Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 20-22.

favorable weather conditions—replete with thermal updrafts—tended to home quicker, due to their inclination to soar along the thermals. Storms inevitably slowed or prevented the returns of both gulls and terns. And finally, birds released near unfamiliar coastlines tended to follow the coast, even if that took them farther from their goal; coasts thus seemed to be an important environmental cue, yet this insight did not clarify the problem of distant homing. The initial results led Griffin to conclude tentatively that birds probably found their way home by a process of random wandering, or exploration, until they reached familiar territory.[59]

Griffin was able to test by direct observation, albeit in a limited fashion, the random exploration hypothesis. The first method involved using a telescope to follow birds after their release, but this failed to yield any helpful data since most birds released on land tended to alight upon the first body of water they reached. Also, the telescope was only good for tracking up to two miles. Following by aircraft proved more fruitful, and using this pioneering method Griffin was able to track the initial homing flights of eight gulls. Although the maximum distance he was able to follow a single bird was 37.5 miles, the results of these observations were useful. He found that rather than flying initially in the direction of home, the gulls did indeed tend to scatter in random directions before wandering. Furthermore, the direction of their scattering did not correlate with the time it took each individual to find its way home. Therefore, the airplane observations seemed to indicate that birds did in fact use some form of random exploration to find their way home.[60]

---

59 Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 31-32.
60 Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 24-27.

Like his previous work on petrels, these experiments raised more questions than they answered. For Griffin, the data seemed to indicate that birds simply "scatter in any direction from the release point and return only when they encounter by chance some part of the area with which they are already familiar."[61] Nothing necessarily indicated that birds flew directly toward home upon being released, and the percent and speed of returns were consistent with the theory of random scattering. Those that happened to choose the correct initial direction may have returned home quicker than those that chose incorrectly, but Griffin could not be certain of this until he conducted more airplane observations.

Griffin thus became convinced—under Lashley's influence—that homing was more complex than a matter of simple sensory mechanisms. Unlike his experiments with petrels, which included extensive testing for orientation by direct vision (landmarks visible at a distance), kinaesthetic memory, and magnetic sensation, Griffin only conducted one sensory isolation experiment on gulls and terns—a rather superficial test for kinaesthesia. These four birds, transported in an unconscious state, were able to return successfully from familiar territory.[62] Griffin was unable to arrange this test from unfamiliar territory, but he assumed that if the kinaesthetic sense played a role in homing at all, then it should be obvious based on experiments in familiar territory. He did not test any birds for magnetic sensitivity, thinking that the evidence in its favor did not warrant further exploration. First, birds possessed very few "ferrimagnetic" substances in their tissues, and consequently they were almost wholly unaffected by magnetic fields.

[61] Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 31.
[62] Donald Griffin, "Homing Experiments with Herring Gulls and Common Terns," p. 30. Griffin noted that two of the anaesthetized birds returned much slower due to being released in a weak condition and in poor weather.

Perhaps more importantly, Griffin reasoned that even if birds did possess a kind of physiological compass, this would not provide them with any information about which direction was home.[63] That is, when carried into unfamiliar territory, birds might be able to determine which direction was north; however, unless they knew the exact route of their outbound journey (and thus which direction they came *from*), that information would not be of much use in guiding them home.[64]

Homing by way of visual exploration thus became Griffin's preferred hypothesis, since he considered it to be the simplest explanation of his results. When he synthesized his data with that of other scientists, including Watson and Lashley, Rüppell, and others, he found that random exploration, as a probabilistic model, seemed to make sense of their data as well.[65] The theories that had been previously proposed to explain migration—namely vision, kinaesthesia, and magnetism—had made little progress in solving the problem. Instead, Griffin suggested, perhaps exploration as the result of radial scattering or in an expanding series of large spirals—which could be efficiently used to survey large areas of unfamiliar territory—could explain homing from unfamiliar territory. For example, if one were to assume that Rüppell's starlings and swallows scattered randomly in a radial fashion, then quicker returns could be explained by assuming that those birds happened by chance to choose an initial direction that pointed them toward familiar territory.[66] Therefore, when Rüppell increased the distance of his releases, the return

[63] Donald Griffin, "The Sensory Basis of Bird Navigation," *Quarterly Review of Biology*, Vol. 19, No. 1 (Mar. 1944): 15-31, p. 25.
[64] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 25.
[65] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 15-31. This article was mostly taken from Griffin's thesis as well.
[66] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 22.

times would still vary arithmetically rather than geometrically, since those birds that returned quickly could simply have taken flight in a fortuitous direction.

Despite the exploration theory's ability to account for the results of several homing experiments, Griffin realized that it did not represent a *total* solution to the problem, since some of the data indicated particularly quick returns from unfamiliar territory. "Exploration may play in important part in the homing of many birds, particularly when speed or per cent returns are low; but it does not seem capable of accounting for all the recorded cases."[67] If these birds returned via exploring, then they did so quickly and efficiently. And although Griffin was skeptical of the evidence that indicated direct or mostly direct routes from unfamiliar territory, he took it seriously.[68]

Turning to Ecology

When his working hypothesis of random wandering and exploration had difficulty accounting for data such as direct returns from unfamiliar territory, Griffin returned his focus to the sensory physiology of birds.[69] However, rather than looking for a specific sensory mechanism that correlated with an explicit environmental cue, he looked for more general environmental cues that birds could use for orientation and navigation. Thus he began to wonder if orientation depended on the perception of "ecological cues" that had yet to be considered.[70] For example, birds "might know the relationship between

---

[67] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 24.
[68] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 22. He specifically cited Rüppell's account of three starlings that seemed to take a straight course home. Although this was a tiny sample, Griffin took it as a potential challenge to the exploratory theory. Werner Rüppell, "Ergebnis eines Heimfindeversuches mit aufgezogen Staren," *Vogelzug*, Vol. 9 (1938): 18-22.
[69] The most compelling evidence of direct returns came in experiments on Manx shearwaters conducted by British ornithologists David Lack and R.M. Lockley: David Lack and R.M. Lockley, "Skokholm Bird Observatory Homing Experiments," *British Birds*, Vol. 31 (1938): 242-248.
[70] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 18.

geographical features such as river systems and coastlines near their home and the direction of sunrise, or sunset, or conceivably of other celestial landmarks."[71] Knowledge of these relationships and of "other ecological and topographical regions" would permit a bird to orient itself in unfamiliar territory by following streams, for example, which flowed downward toward the coastline.[72] Thus Griffin suggested that the relationship of the physical stimulus to the bird's perception was more complex than simple cues, visual or otherwise.

With Lashley's guidance, Griffin began to pursue further the idea that birds perceived structural, or environmental, relationships in their landscapes, which helped them acquire information about where to go. For example, he suggested that migration might be considered an instinctual behavior—"in the meaning defined by Lashley (1938)"—insofar as it was guided by the bird's use of environmental and geographical cues to navigate its course.[73] In that 1938 essay, cited by Griffin, Lashley argued that the nature of the visual stimulus, rather than being simple, instead involved the perception of complex holistic qualities that were reminiscent of forms in Gestalt theory.[74] Lashley further explained that "psychological theories based upon the relations of stimulus and response remain sheer nonsense so long as the stimulus is defined only as whatever the experimenter puts in front of the animal…In any complex situation the true basis of reaction can be discovered only by systematic variation of all the parts and properties of the supposed stimulus."[75] As a consequence, simplistic conceptions of stimulus and

---

[71] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 29.
[72] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 29.
[73] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 28. Karl Lashley, "Experimental Analysis of Instinctive Behavior," *Psychological Review*, Vol. 45 (1938): 445-471.
[74] Karl Lashley, "Experimental Analysis of instinctive Behavior," *Psychological Review*, Vol. 45 (1938): 445-471.
[75] Karl Lashley, "Experimental Analysis of Instinctive Behavior," p. 455.

response failed to capture that which was "so complex and precise in its execution that we can only stand aghast at the inadequacy of our concepts of its mechanism."[76] In essence, his concept of instinct thus complemented its classical definition: "the faculty which animals have instead of intellect which yet make their behavior seem intelligent."[77]

Lashley's ideas about animal instinct and perception shaped how Griffin interpreted the results of his experiments. Thus Griffin came to understand orientation and navigation in terms of the bird's perception of more general environmental cues: "The combined use of familiar landmarks, together with simple geographical, meteorological, and ecological relationships such as those described above seems more reasonable as an explanation of migration and homing than the postulate of a new sense organ."[78] These new ideas also began to shift Griffin's understanding of what constituted 'familiar' territory. Before this point he had understood it to mean that which the bird had visited before and remembered; thus the bird recognized landmarks encountered in its previous travels and oriented itself toward more distant goals based on those. In developing these new ideas about exploration, Griffin postulated that a bird might recognize certain *types* of landscapes or environmental cues; even if it had no visual memory of a particular river system, for example, it might recognize that river systems in general tended to flow toward coasts. And previous homing experiments had suggested that birds tended to home faster the nearer they were to coasts, since they were often more familiar with coastal territory. These environmental cues also included weather and wind patterns that were characteristic of certain environments, and the bird could leverage its familiarity with such cues in order to navigate unfamiliar territory more

[76] Karl Lashley, "Experimental Analysis of Instinctive Behavior," p. 446.
[77] Karl Lashley, "Experimental Analysis of Instinctive Behavior," p. 446.
[78] Donald Griffin, "The Sensory Basis of Bird Navigation," p. 29.

effectively. Griffin explained his ideas directly in a letter to his colleague Dave Davis, who also worked on migration:

> The ideas are very vague and need much more work to confirm them before they would have any significance, but this is it in brief: that birds recognize air masses by stability (presence or absence of updrafts), temperature, humidity, visibility, cloud types, and possibly other factors, and also "know" that within each air mass there are strong tendencies for prevailing winds […] Translating this into a herring gull's point of view, clear cool days with good soaring occurs when the winds are from the land towards the coast. If he flies inland on such a day he gets back by soaring and letting himself be carried downwind; if he is shipped in a crate to Lake Erie and finds such weather he also soars downwind and eventually reaches the coast, much of which he knows from previous wanderings and migrations. This is of course all stated in terms of local conditions and one species, but this sort of explanation seems much more reasonable to me than magnetic senses, etc.[79]

Although in this passage Griffin focuses mostly on the perception of weather patterns, he conceived that birds would similarly perceive visible aspects of their environments (wooded areas, river systems) in order to "know" about where to fly in unfamiliar territory. While little direct evidence pointed toward a full solution, the breakdown of simpler, mechanistic possibilities opened up the creative space for Griffin to develop these ideas.

Griffin received his PhD in the spring of 1942, and planned to extend his study of bird migration in order to better understand the problem. The next step was practical and technical: he planned to follow birds from airplanes, chart their exact routes, and attempt to correlate homing performance with the birds' ability to perceive more general features of, or types of landscapes along their routes. However, the United States' entry into World War II and Griffin's subsequent years of military research delayed this project. At the war's conclusion, Griffin decided that it was best to use the remainder of his Junior

[79] Donald Griffin to Dave Davis, 12 July 1942, Series 1, Box 2, Folder [Corr. Da-DeZ], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

Fellowship at Harvard to explore bat echolocation. As demonstrated in the previous chapter, his wartime investigations sparked new insights about echolocation, and so after the war he returned to his first love, bats. Then in July of 1946, he took a job at Cornell, where he became an assistant professor of physiology. His first year was frantically busy, as he prepared to teach courses in general and comparative physiology, but in the summer of 1947, Griffin was finally able to return to the problem of bird navigation.

By this time, Griffin had fully confirmed his view of bird migration as both a physiological and an ecological problem.[80] That is, he thought that birds navigated not by a "unique sensory mechanism, but rather by an ability to perceive environmental cues which are within the scope of the receptors common to all higher vertebrates."[81] When displaced into unfamiliar territory, birds simply explored until they came upon a familiar landmark, or an environmental cue that might lead them toward familiar territory: "When landmarks (rivers, coastlines, mountain ranges, etc.), prevailing winds, or the direction of the sun are not available as guiding influences, or when birds are released in unknown territory where the environmental cues have no meaning, they may well reach their goal by a process of exploration."[82] Since nearly all homing data could be explained by assuming that birds did not fly directly home from unfamiliar territory, but instead explored large areas before finding their way home, Griffin needed to follow birds in order to chart and to make sense of their explorations. He sought to discover whether there were structural or environmentally determined patterns to their exploratory flights,

---

[80] Donald Griffin and Raymond J. Hock, "Airplane Observations of Homing Birds," *Ecology*, Vol. 30, No. 2 (Apr. 1949): 176-198. This was Griffin's first publication in the journal *Ecology*. The work was funded by a grant from the Office of Naval Research.
[81] Donald Griffin and Raymond J. Hock, "Airplane Observations of Homing Birds," p. 176.
[82] Donald Griffin and Raymond J. Hock, "Experiments on Bird Navigation," *Science*, Vol. 107, No. 2779 (Apr. 1948): 347-349.

and so once again he designed homing experiments from unfamiliar territory that he could follow by plane. By this point, Griffin had learned to pilot the aircraft himself, and in the experiments he was joined by Cornell graduate student Raymond J. Hock.

Gannets were well suited for homing experiments, since they spent most of their time near the shore. Any releases from inland points, therefore, would place the birds into what was almost certainly unfamiliar territory. Furthermore, with large, white bodies, and a 5-6 foot wingspan, they were easy to spot from low-flying airplanes. Finally, they gathered in large numbers on Bonaventure Island in Quebec, not too far from Ithaca. Griffin and Hock captured several gannets and transported them in covered cages to the Caribou, Maine regional airport, near the border of Canada. The plan was to track each bird from 2,000 feet above and to plot its course. After takeoff, an assistant at the airport hangar released the gannets one at a time, and Griffin and Hock tracked them for as long as they could.[83] Many of the flights were cut short by losing sight of the birds, and the rest were concluded due to loss of daylight or fuel concerns.

They followed nine birds in total, and released eight controls that were not followed. The gannets were apparently undisturbed by the plane when it flew above, and the controls, released from the same point, ensured that the presence of the aircraft had not fundamentally skewed the results.[84] Both the observed and control groups performed similarly: about 60% of them found their way home in times ranging from 24-100 hours. The similarity in performance gave Griffin confidence that the birds had not been

[83] This was somewhat tricky and it involved taking many trips back and forth by plane to Bonaventure Island to capture fresh birds, because Griffin did not want to hold any single bird in captivity for too long. The average captivity time was about 29 hours: birds held this long were still in good condition upon release.

[84] Because the birds flew slower than the plane, Griffin and Hock flew above the birds in large circles so that they could maintain their flight speed and still keep an eye on the birds.

disturbed by the aircraft. While tracking, he paid close attention to the local topography, including streams, valleys, and wooded areas. He also kept detailed notes about the weather conditions, including the direction of the wind at the time of release. The best homing performances, they found, were in favorable weather conditions—clear skies, winds blowing in the home direction, and plenty of updrafts (since gannets, like gulls, prefer soaring).[85]

Griffin described in some detail the paths of tracked birds that homed successfully, noting for example, whether the bird's behavior changed upon encountering new topographical features. In one telling instance, they followed a gannet that did seem to indicate some sort of environmental recognition. This bird flew east from the airport toward the Gulf of St. Lawrence for about five hours. As Griffin and Hock first arrived at the Gulf's inlets, "at almost the same moment…the bird rather suddenly dropped to below 2,000 feet. Probably the ocean was visible to the gannet as soon as to us…As it approached the shore, the bird turned gradually north and dropped still lower...to investigate the salt water. It seemed as though it recognized the ocean, for it certainly altered its flight on approaching it."[86] Their observation was cut short, but the bird did eventually return successfully, albeit it in an amount of time indicating that it did not fly home directly. While this observation was hardly a smoking gun, it did indicate that birds reacted to changes within environments that were probably unfamiliar to them.

On the whole, however, the paths taken by gannets did not seem to follow a fixed structure, nor were they greatly affected by topographical or environmental elements. When plotted on a map, none of the gannets showed evidence of spiral exploration either.

---

[85] Donald Griffin and Raymond J. Hock, "Airplane Observations of Homing Birds," p. 197.
[86] Donald Griffin and Raymond J. Hock, "Airplane Observations of Homing Birds," p. 187.

Rather, the birds took seemingly random paths and were only able to return after dozens of hours of exploration. This seemed to confirm the exploratory theory. One important finding, however, was that the gannets that reached the coast relatively quickly found their way home sooner. Griffin supposed that this probably was due to the fact that they were most accustomed to life on the shores, and had come into contact with familiar territory once they started following the coasts. The experiments, however, provided few clear answers. As Griffin explained, "one salient and simple fact emerges from a study of these data – the gannets did not fly at all directly home."[87] Essentially, he was back to square one.

When Griffin began his migration research in 1938, he looked for simple sensory mechanisms to explain homing. This was in accordance with the mechanistic framework of animal behavior that he had learned in his undergraduate years at Harvard. With Lashley's guidance in further experiments, he came to see the bird's use of environmental cues as an exploratory process, rather than one based on stimulus-response mechanisms. Thus by the mid 1940s Griffin's approach to the problem of homing and navigation had become equal parts physiological and ecological. Although he still understood the ability to be a matter of sensory physiology—that is, not one of cognition or consciousness—he began to expand his view of what constituted an environmental cue, and how birds explored their environments using the traditional senses. His new understanding of environmental cues included holistic phenomena such as general weather patterns, and structural features of unfamiliar landscapes such as river systems and coastlines. Rather than positing some mysterious sense, he argued that birds merely explored unfamiliar territory and looked for general features that might lead them homeward.

[87] Donald Griffin and Raymond Hock, "Airplane Observations of Homing Birds," p. 190.

For Griffin, the exploratory theory did not constitute a complication of the problem; rather, he considered it to be the most conservative interpretation of his experimental data. Not only did the theory make sense of his data, it did not require positing unknown, or unproven sensory mechanisms. For him, this conservative approach constituted good science: it restrained the imagination, attempted to account for animal behavior using known sensory mechanisms, and restricted the interpretation of experiments to the simplest explanation supported by the data. As a consequence, Griffin was very surprised in the late 1940s to learn of a new theory, which once again claimed to explain orientation as a simple matter of magnetic sensation.

Magnetic Orientation and the Yeagley Controversy

For Griffin, the problem of bird navigation became even more urgent when a new theory of magnetic homing in pigeons was proposed by physicist Henry Yeagley in 1947. Griffin had actually done preliminary research on pigeons upon arriving at Cornell in the fall of 1946, although that work had failed to shed any new light on the problem of navigation.[88] Over the course of these brief investigations, however, Griffin began seeking the advice of Yeagley, an expert on pigeons at Pennsylvania State College.[89] During the war, Yeagley had become closely associated with the Army Signal Corps' pigeon group in Ft. Monmouth, New Jersey. The head of the pigeon group, Major Otto Meyer, advocated Yeagley's wartime work, which was supported by military dollars.

---

[88] Like his work on gannets, Griffin tried to determine if pigeons used environmental cues to navigate from unfamiliar territory. He found, however, that pigeons required training and familiarity in order to home, and that they were generally very poor at homing from unfamiliar territory. He did not publish his findings until several years later, when the Yeagley controversy had become quite pronounced. Donald Griffin, "Airplane Observations of Homing Pigeons," *Bulletin of the Museum of Comparative Zoology*, Vol. 107 (1952): 411-440.

[89] Pennsylvania State College became a university in 1953.

Griffin first wrote to Yeagley in the fall of 1946 to inquire about purchasing pigeons for homing experiments at Cornell. In turn, Yeagley revealed that during the war he had found a solution to the problem of orientation that involved the perception of the Coriolis force and terrestrial magnetism: "Our work started in 1943 with a proposed theory involving the vertical component of the earth's magnetic field intensity and the Coriolis effect associated with the earth's rotation…Because of the military importance of the findings, our reports have all been of the restricted class and were released only to the Army Service Forces of the Army Signal Corps."[90] Yeagley explained that it was now time to go public with his findings, since the war had ended and his results were "very strongly indicative of the validity of the theory."[91] Griffin was intrigued, but skeptical. Magnetic theories were hardly new, and nearly all the evidence he had come across militated against it. He wrote to Yeagley a few days later, explaining that his initial experiments on pigeons seemed to indicate that their homing could be explained on the basis of familiarity with landmarks, which they acquired during training exercises. Perhaps this ability could be accounted for "on the basis of learning of other sensory cues such as magnetic ones," but Griffin doubted they were necessary.[92] Nevertheless, much of Yeagley's theory depended on arcane physical calculations, and so Griffin decided to withhold further judgment until the work was published.

Their correspondence trailed off shortly thereafter, and Griffin ceased most of his pigeon work in 1947 when he had the opportunity to study gannets. As he explained,

---

[90] Henry Yeagley to Donald Griffin, 31 October 1946, Series 1, Box 12, Folder [Y-Z], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[91] Henry Yeagley to Donald Griffin, 31 October 1946, Series 1, Box 12, Folder [Y-Z], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[92] Donald Griffin to Henry Yeagley, 5 November 1946, Series 1, Box 12, Folder [Y-Z], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

gannets were more intriguing since they were naturally migratory and undomesticated: "the studies with wild birds are somewhat more closer to my interests, and I think they will be more profitable from my point of view."[93] Then in the late-summer of 1947, Griffin went to the Arctic Research Laboratory in Pt. Barrow Alaska on a grant from the Office of Naval Research. In addition to basic research on physiological thermodynamics, he conducted homing experiments on arctic terns and plovers.[94] While there, he received word from colleagues that Yeagley had begun to discuss his magnetic theory publicly, although it had not yet been published.

Yeagley's theory was first published in December of 1947 in the *Journal of Applied Physics*. The problem of orientation was complex, Yeagley explained, but he and his colleagues had discovered a rather straightforward solution. It held that migratory birds—not just the pigeons on which his research was based—possessed an organ or organs that were sensitive to two main sensations: the electromagnetic effects generated by the bird's motion through the earth's magnetic field, and "the effort exerted to overcome the Coriolis force, due to the earth's rotation."[95] The Coriolis effect, generated by the rotating earth's centripetal force, varies in its intensity between the poles, where it is greatest, and the equator, where it is zero. According to Yeagley, birds could determine their latitude based on differences in the strength of the force. The theory also held that

[93] Donald Griffin to Henry Yeagley, 3 June 1947, Series 1, Box 12, Folder [Y-Z], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[94] In this work Griffin took advantage of wartime developments in radioisotopes. He devised a system that placed a small radioisotope around the collar of birds, which would be detected by a Geiger counter under their nests. The counter was connected to a chronometer that noted the time when the bird returned to its nest, thus setting off the Geiger counter. Donald Griffin, "Radioactive Tagging of Animals Under Natural Conditions," *Ecology*, Vol. 33, No. 3 (Jul. 1952): 329-335.
[95] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," *Journal of Applied Physics*, Vol. 18, No. 12 (Dec. 1947): 1035-1063. Swedish geophysicist Gustav Ising proposed a similar theory of Coriolis orientation around the same time: W.H. Thorpe, "Ising's Theory of Bird Orientation," *Nature*, Vol. 158, No. 4025 (Dec. 1946): 903-904.

birds were "visually sensitive" to their own "velocity over the earth's surface (land speed)."[96] They supposedly used a comparison of their groundspeed with that of their absolute velocity, which was affected by the Coriolis effect, in order to orient themselves. The perception of these forces apparently created a navigational grid on which birds oriented their horizontal and vertical position on the earth's surface. While Yeagley had yet to demonstrate the existence of the organ or organs involved, he claimed that experiments on homing pigeons validated the theory.

Previous theories had attempted to calculate the effects of a stable magnetic field, but Yeagley's theory was based on the electromagnetic force generated by the bird moving through the earth's field. Displaced birds, he supposed, could make adjustments in their flight "in a direction which will bring its land-speed magnetic vertical-field effect back to that to which it is accustomed during its normal flight and home territory."[97] Essentially, birds would become accustomed to the magnetic and rotational forces characteristic of their home territories. When they flew in unfamiliar territory, they adjusted the direction of their flight in order bring the sensation of these forces into alignment with that of their home territory.[98] Ultimately, the relationship between the magnetic and Coriolis forces would provide the bird with a grid on which it oriented itself toward home territory.

A corollary to the theory, Yeagley explained, was that due to the distribution of the earth's magnetic field and the properties of Coriolis velocity between the poles and the equator, there should be several points on the earth's surface that were characterized by the same ratio of magnetic to Coriolis force. He termed these "conjugate points," and

---

[96] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1037.
[97] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1039.
[98] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1039.

plotted them on a map of the United States.[99] At each conjugate point, the intersecting lines of magnetic and Coriolis force were identical, and thus from the bird's perspective, the navigational cues should be identical.

Yeagley's article included details of several experiments with pigeons that supposedly demonstrated the importance of these forces in orientation. His "magnetic wing" experiment, for example, showed that when magnets were attached to the wings of pigeons, their homing ability was disrupted.[100] Of the ten magnetized pigeons that he released into unfamiliar territory, none returned, and initial observations indicated that most of them did not immediately fly in the home direction. Ten control pigeons had similarly sized copper plates (nonmagnetic) attached to their wings, and their homing performance was significantly better: eight of ten returned within two days.[101] Yeagley argued that this was sufficient to demonstrate that pigeons could perceive significant magnetic forces, and that the ability to perceive those forces affected homing performance.[102] The crucial experiment, however, involved the conjugate points.

Yeagley hypothesized that if a bird were displaced into unfamiliar territory that was near a conjugate point, then it would mistake that point for its home territory and navigate towards it. Thus he trained several hundred birds to home toward a mobile loft near campus in State College, Pennsylvania. While training his pigeons in Pennsylvania, Yeagley occasionally moved the mobile loft to different locations so that the birds became "accustomed to looking for the loft and not for familiar landmarks nearby."[103] According to the U.S. Coast and Geodetic Survey Map, there was a conjugate point for

[99] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1039.
[100] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1042-43.
[101] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1043.
[102] He did not perform an equivalent experiment to test for Coriolis perception.
[103] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1045.

State College ten miles north of Kearney, Nebraska.[104] The plan was to release 120 pigeons, which had been trained to home toward their loft in State College, at points surrounding the conjugate. Each bird was tagged with instructions for reporting the recovery data so that Yeagley could determine if it had taken a relatively straight course (a "vector") between the release point and its "home" loft at the conjugate point. In the summer of 1944, Yeagley's team released eight groups from their displacement points. Only one bird actually returned to its loft, but about fifty others were recovered and recorded in various locations. Recoveries within 25 miles of the lofts were interpreted as successful homing. Yeagley averaged the data based on the recovery locations, trajectories, and speeds of the birds in each group, and from this he plotted the vector of the group. According to Yeagley, six of the eight vectors pointed toward the conjugate point, thus supporting his theory.[105]

Further experiments in the summer of 1945 increased the number of pigeons to 200. These tests involved "handicapping" the birds in order to secure more trustworthy conclusions. This was accomplished by training the birds to home solely from points northwest of their Pennsylvania lofts. In the Nebraska experiments, these birds were released northeast of the conjugate point. In this way, it was thought that any directional habituation would be disrupted; if the birds did fly toward the conjugate point, Yeagley reasoned, he could be confident that they did so according to his theory.[106] After being released, 32% of the birds were recovered at various points in the surrounding areas; none were recovered at the lofts. When analyzing the data, Yeagley curiously excluded

---

[104] Due to magnetic anomalies in the local conditions, there were actually two conjugate points near Kearney, about 25 miles apart. Yeagley set up return lofts at both locations to be safe.
[105] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1049.
[106] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1056.

all the recoveries that had taken place ten or more days after the release. Based on the reports of racing pigeon fanciers, he assumed that after a period of ten days, these birds would have given up on trying to find their way home, and had probably flown off in random directions. The vectors established by the recoveries confirmed the earlier experiments, as most of them pointed toward the conjugate point.[107]

Yeagley concluded that his experiments had gone a long way toward solving "the age-old mystery of bird migrations."[108] Despite the fact that virtually no direct evidence demonstrated that pigeons were physiologically capable of perceiving magnetic or Coriolis forces, Yeagley based his conclusion on the homing experiments and on the limited "magnetic wing" experiments. His method of averaging bird recoveries into vectors also seemed quite suspect, as he used these to conclude that pigeons were homing toward the conjugate points even though very few pigeons were actually recovered near the loft. Finally, his assertion that he had solved—or at least "clarified"—the whole problem of bird migration in experiments on *trained pigeons* was certainly problematic.

Not surprisingly, Yeagley's theory was truly exciting to those scientists working on the problem of homing and migration. It was widely disseminated and discussed, and many initially welcomed the elegant solution that he had found via seemingly rigorous experimentation. The theory was simple, physiologically and physically grounded, and clarified a complex behavioral problem in such a way as to suggest further investigation. Within a few years, however, physicists, physiologists, ecologists, and ornithologists alike discovered numerous problems with Yeagley's methods, interpretations, biological and physical assumptions, and most importantly his sloppy research practices. By the

---

[107] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1057-1062.
[108] Henry Yeagley, "A Preliminary Study of a Physical Basis of Bird Navigation," p. 1062.

early 1950s, this litany of negative criticisms had largely discredited his work and reputation. Griffin was central to the critical response.

An Unwelcome Theory: The Skeptics Respond

Griffin was already skeptical of magnetic orientation theories, and of Yeagley's in particular, especially upon receiving an advance copy that Yeagley sent him in October of 1947.[109] For Griffin, magnetic theories of orientation harkened back to Loebian conceptions of behavior as the product of simple and automatic stimulus-response mechanisms. By the late 1940s, he had begun to see animals as more complex agents that explored their environments while acquiring and processing information that informed their patterns of behavior.[110] Thus Griffin firmly rejected both Yeagley's faulty methods and wild assumptions, but more importantly his tropistic formulation of the problem of migration. He would wait several years until publicly disclosing his problems with the theory, but in the interim, Griffin privately discussed its problems with others in the field, many of whom issued published criticisms.

One of the major problems that Griffin immediately noticed involved publicity surrounding the conjugate experiments in Kearney, Nebraska. A few weeks after the theory became public, he wrote to German ornithologist Erwin Stresemann (1889-1972), who in the 1930s had also proposed a magnetic theory of orientation.[111] Griffin doubted Stresemann's theory as well, but he explained to him that corrupt records of Yeagley's

---

[109] Henry Yeagley to Donald Griffin, 29 October 1947, Series 1, Box 12, Folder [Y-Z], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[110] Karl von Frisch's work on the solar orientation and dance language of the honeybees had an important influence on Griffin's thinking. My next chapter explains this in greater detail.
[111] Erwin Stresemann, "Haben die Vögel einen Ortsinn?", *Ardea*, Vol. 24 (1935): 213-226.

pigeon returns near the conjugate point had probably skewed the results.[112] "You would be interested in Yeagley's work with pigeons, although I am most skeptical of his conclusions…I feel that the results could be due to the newspaper and radio publicity asking people to be watching for pigeons, since this probably centered around the 'conjugate point', but this is only my personal opinion."[113] Despite the fact that only about 25% of the pigeons released were recovered and reported in those experiments, Griffin thought that the public, on whom the experiments relied to help with pigeon recoveries, would be more inclined to look for pigeons near the conjugate point where they were predicted to be. The fact that publicity about the experiments (which called for the public's assistance) was limited to the immediate area around the conjugate point was even more problematic. A few months later Griffin wrote to Yeagley, inquiring further about the nature of the publicity and other problems that had been raised against his theory.[114] Yeagley replied, explaining that they had considered generating wider publicity in order to increase the returns, but because their work was "an Army project of the restricted classification," they limited their publicity to the areas surrounding the conjugate point.[115]

Just a few days after receiving that rather unsatisfying explanation from Yeagley concerning the nature of publicity about his experiments, Karl Lashley wrote to Yeagley and carbon-copied Griffin. Lashley's handwritten preface to Griffin explained, "Yeagley's study seems to include a lot of post hoc explaining and special pleading. The

[112] Donald Griffin to Erwin Stresemann, 29 December 1945, Series 1, Box 10, Folder [Sn-Sw], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[113] Donald Griffin to Erwin Stresemann, 29 December 1945, Series 1, Box 10, Folder [Sn-Sw], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[114] Donald Griffin to Henry Yeagley, 12 February 1948, Series 1, Box 12, Folder [Y-Z], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[115] Henry Yeagley to Donald Griffin, 28 February 1948, Series 1, Box 12, Folder [Y-Z], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

theory seems physiologically impossible and I am not impressed by this evidence."[116] In the body of the letter, Lashley explained to Yeagley that his theory was merely the latest in a long line of attempts to explain bird migration by positing the existence of mysterious abilities:

> My feeling, after following work on homing for many years, is that there has been a tendency to exaggerate the mystery, as there has been in the case of supposed telepathic phenomena, with a similar mystical reluctance to accept commonplace explanations…I see no reason to look for other explanation than a good topographic memory (even wasps show this within limited range), good 'woodsmanship', and random wandering.[117]

He further explained that Yeagley had not demonstrated that the perception of magnetic and Coriolis forces was anatomically or physiologically possible, and that "for these biological reasons your assumptions seem to me extremely improbable." In three richly detailed pages, Lashley went through each of Yeagley's experiments, pointing out problems with his assumptions, methods, and interpretations. He held nothing back, explaining that Yeagley's vector numbers, which were too minimal to be trustworthy in the first place, could further be explained by the existence of the Platte River near the conjugate point. Lashley explained that migration routes and other experiments had demonstrated that "coastlines, mountains and rivers play a part in bird navigation." Several releases, therefore, may simply have followed the river rather than a magnetic sense, thus yielding the vector data. Hence Yeagley's results were "meaningless."

Yet another problem was the way Yeagley interpreted the recoveries. One group of birds, for example, was released about 60 miles east of the conjugate point, and was recovered 100 miles west of the point. They were therefore recovered farther from the

[116] Karl Lashley to Henry Yeagley [CC: Donald Griffin], 2 March 1948, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[117] Karl Lashley to Henry Yeagley [CC: Donald Griffin], 2 March 1948, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

conjugate point than they were released, but because of the way Yeagley calculated the vectors, the apparent direction that the birds took upon being released was toward the conjugate point. Thus he included it as positive evidence. Lashley concluded, "Much of this may seem like quibbling but I want to emphasize that in studies of this sort there are many variables which must be considered; topography, opportunities for feeding, distribution of human and hawk populations, prevailing wind directions, etc., none of which have been even referred to in your study."[118] One of Lashley's most significant criticisms, therefore, was that Yeagley had approached the problem as one of physics, rather than as one of ecology and zoology. Apparently Yeagley never responded: "He asked me for criticism but apparently did not like what he received."[119]

Griffin thanked Lashley for copying him on his "masterly letter to Yeagley regarding his crazy theories."[120] The theory and Yeagley's experimental findings, as Lashley mentioned at the outset, were improbable for "biological reasons." Perhaps Yeagley decided not to respond because Lashley's criticisms were so comprehensive and delivered in such an unambiguously critical tone. Or maybe he felt incapable of responding to the biological objections raised against his theory. Nevertheless, there were physical and theoretical problems as well, and the physicists in fact were the first to challenge the theory publically.

---

[118] Karl Lashley to Henry Yeagley [CC: Donald Griffin], 2 March 1948, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[119] Karl Lashley to Donald Griffin, [Undated] December 1948, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[120] Donald Griffin to Karl Lashley, 21 December 1948, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

These first printed criticisms were included in the very next issue of *The Journal of Applied Physics*, in March of 1948.[121] Three physicists—Joseph Slepian, Russell Varian, and Leverett Davis—offered separate but related critiques of Yeagley's work. Slepian focused on the claim that birds perceived electromagnetic forces generated by their motion through the earth's magnetic field. According to the theory of relativity, he explained, the bird's uniform motion through the earth's magnetic field would not produce an electromagnetic force distinguishable from a resting state. Hence, it would not perceive magnetic forces merely by virtue of its motion. Furthermore, any magnetic effects that the bird could possibly perceive would be "completely overshadowed and obliterated by the indistinguishable 'sensitivity' to changes in the earth's horizontal field."[122] According to Slepian, the "intensity of the earth's electric field is normally thousands of times larger" than the effects that the birds supposedly perceived. Therefore, in order for the theory to work, birds would have to be sensitive to the earth's magnetic field itself, not to the effects of their own motion through the field.

Stanford physicist Russell Varian offered a similarly devastating critique, arguing that Yeagley had jumped "to unwarranted conclusions concerning the operation of these senses."[123] Varian reiterated Slepian's criticism based on relativity, and further charged that Yeagley's Coriolis assumptions were faulty. As Varian explained, the pigeon's ability to orient itself within 25 miles on the grid would require it to sense extremely minute gravitational accelerations. He concluded, "this appears to be practically

[121] Joseph Slepian, Russell Varian, and Leverett Davis, "[Letters to the Editor] Remarks on 'The Physical Basis of Bird Navigation,'" *The Journal of Applied Physics*, Vol. 19, No. 306 (Mar. 1948): 306-308.
[122] Joseph Slepian, "Physical Basis of Bird Navigation," p. 306.
[123] Russell Varian, "Remarks on: 'A Physical Basis of Bird Navigation,'" p. 306.

impossible, even though it may be theoretically possible."[124] He further doubted that an organ sensitive enough to make such discriminations would have ever had enough survival value to become further improved by natural selection. Leverett Davis, a physicist at California Institute of Technology, offered the final critique. He reiterated Slepian's and Varian's objections concerning the perception of minute forces, but suggested that pigeons might still be able to determine their latitude by observing the position of the sun and stars. He then suggested some experiments to help refine the problem since he thought it was "desirable to test such a remarkable theory in as many ways as possible."[125]

Coming as they did from within the physics community, these critiques certainly painted Yeagley's theoretical claims in a negative light. In April of 1948, the renowned ecologist G. Evelyn Hutchinson further challenged Yeagley's assumptions about the birds' perception of what must be, according to physical laws, the exceedingly minute electromagnetic and mechanical effects proposed by the theory.[126] "The chief difficulties," he explained, "are of a theoretical and physiological nature." Hutchinson was willing to grant the validity of Yeagley's experimental findings, and in fact he congratulated him on the work. But he doubted Yeagley's physiological assumptions about the perception of magnetism and the Coriolis effect.[127]

Other responses from biologists and ecologists were more damning, and focused almost entirely on flaws in Yeagley's methods. Evolutionary biologist V.C. Wynne-Edwards, for example, charged that Yeagley's primary statistical metric—combined

[124] Russell Varian, "Remarks on: 'A Physical Basis of Bird Navigation,'" p. 306.
[125] Leverett Davis, "Remarks on: 'The Physical Basis of Bird Navigation,'" p. 306-307.
[126] G. Evelyn Hutchinson, "Marginalia," *American Scientist*, Vol. 36, No. 2 (Apr. 1948): 218-222.
[127] G. Evelyn Hutchinson, "Marginalia," p. 220.

“vectors”—were wholly inadmissible for two reasons.[128] The first concerned the way that Yeagley obtained the average direction and distance that pigeons took in homing toward conjugate points. As Wynne-Edwards cleverly explained: “If one bird after release goes in the right general direction, misses the loft and continues on ten times too far beyond it, and five others travel in the opposite direction to lesser distances, then the vector-sum of all their efforts combined comes out exactly right as to distance and direction.”[129] The vectors, therefore, did not accurately represent the actual mean course adopted by the pigeons. Furthermore, Wynne-Edwards explained, Yeagley had not employed a control group. The controls should have been released in unfamiliar territory that was not near a conjugate point, in order to measure whether or not they homed in a similar fashion.

Another problem was due to the logarithmic nature of sensory perceptions. According to Wynne-Edwards, Yeagley’s theory held that pigeons would have to sense whether they were getting “hotter or colder” in searching for their home territory. However, due to the extremely small fluctuations that pigeons were supposed to sense, it was “physiologically unlikely, to put it conservatively, that the nervous system could comprehend changes in mechanical and electrical stimulation such as occur over an interval of say 15 miles.”[130] Therefore, the directional precision required by Yeagley’s definition of good homing far outweighed the physiological precision that was capable of being generated by the perception of forces. He concluded the critique by reiterating Griffin’s 1944 assessment that the problem of navigation was essentially one of exploration, not of finding a previously unknown sensory mechanism: “As Dr. Donald

[128] V.C. Wynne-Edwards, “Special Review: Yeagley’s Theory of Bird Navigation,” *Ibis*, Vol. 90, No. 4 (Oct. 1948): 606-611.
[129] V.C Wynne-Edwards, “Special Review: Yeagley’s Theory of Bird Navigation,” p. 610.
[130] V.C Wynne-Edwards, “Special Review: Yeagley’s Theory of Bird Navigation,” p. 610.

Griffin concluded…we must seek what satisfaction we can in explanations based on known senses, especially vision, together with such adjuncts as, for example, the sense of daylength and elapsed time…Griffin and Hock's [work on gannets] lends very strong support to the view that the first steps in orientation are made by random exploration."[131]

A few months later, ecologist H.T. Odum offered a synthetic review of the controversy, and he took a similar position in preferring Griffin's theory to Yeagley's.[132] Odum's critique was particularly devastating, as he characterized most of the conclusions as fundamentally flawed or insubstantial. He mostly reiterated the critiques of previous writers, but he did so assessing each of Yeagley's individual experiments and pointing out their many flaws. As Odum explained, several unacknowledged factors could have skewed the results of the conjugate experiments, such as the existence of a river system that birds could have followed, in addition to weather patterns that may have led to favorable results. In any case, the results were not even that favorable: "if this magnetic effect is a valid one it is not possible to tell from these experiments whether there is any real aid to the bird. As Griffin has shown, a wandering search by the birds could get them home quicker than the time of this experiment. Yeagley's experiments don't tell us which is the case."[133] Odum also attacked Yeagley's theoretical assumptions, especially when it came to the Coriolis force. As he argued, the atmosphere contains numerous pressure gradients that the birds must fly through, and the effects of these would surely dominate a bird's perception of the mechanical forces impinging on its body.[134] Odum concluded by reiterating his preference for Griffin's exploratory theory: "The wandering and visual

[131] V.C Wynne-Edwards, "Special Review: Yeagley's Theory of Bird Navigation," p. 611.
[132] H.T. Odum, "The Bird Navigation Controversy," *The Auk*, Vol. 65, No. 4 (Oct. 1948): 584-597.
[133] H.T. Odum, "The Bird Navigation Controversy," p. 589.
[134] H.T. Odum, "The Bird Navigation Controversy," p. 592.

orientation theory is certainly part of the correct explanation. The magnetic theory is lacking…and upheld by experiments which for various detailed reasons need to be repeated. Even if valid magnetic effects exist, that they are anything but grossly inefficient has yet to be shown."[135]

While Griffin did not issue a formal rejection of Yeagley's theory, he privately disparaged it in correspondence with numerous individuals who were interested in bird migration. Griffin's colleague Harold Hitchcock (1903-1995), for example, had conducted some initial homing work with pigeons at Middlebury College, where he was a professor of biology.[136] Hitchcock was evidently more impressed than his colleagues by Yeagley's work, and Griffin attempted to convince him of its numerous problems. In December of 1948, he complained, "I think Odum's criticisms were very kind, and Odum omitted necessarily some of the most damaging considerations."[137] He then explained what Odum had missed. First, Griffin attacked Yeagley's "magnetic wing" experiment, which supposedly demonstrated that attaching magnets to the wings hindered their homing ability. Griffin noted that in a private conversation, Yeagley apparently admitted that he had attached the magnets by passing wires through the flesh of the pigeon's wings, a method he had not used to attach the copper controls.[138] This of course increased the chances of injuring the pigeon, which undoubtedly could have explained its relatively poor homing performance. Even worse, Griffin explained, was that Yeagley failed to mention this in the paper. Yeagley also apparently miscalculated the magnetic effects of

[135] Howard T. Odum, "The Bird Navigation Controversy," p. 596.
[136] At Harvard, Griffin was friends with Hitchcock, who took his Ph.D. in biology in 1938.
[137] Donald Griffin to Harold Hitchcock, 6 December 1948, Series 1, Box 5, Folder 61, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[138] These conversations took place in the fall of 1946 when Yeagley visited Cornell. Griffin's correspondence with Yeagley intimates that they met briefly, but I have found no direct evidence to characterize those meetings.

the attachments, and he failed to report the results of running the experiment a second time, in which none of the magnetized or control birds returned. Moreover, when Griffin studied the vector maps, he realized that the average deviation of the vectors, which were interpreted to indicate the direction of the conjugate points, was barely better than chance. Even more damning was the fact that most of the birds "averaged farther from conjugate point [sic] after their flights than when released."[139] If anything, this indicated that the pigeons flew *away* from the conjugate points, not toward them.

Around the same time in October of 1948, Griffin's colleague Ed Folk attempted to arrange a public debate between Yeagley and Griffin at Bowdoin College, where Folk worked. Griffin replied, "Regarding a debate with Yeagley I am a little hesitant. By this time I have strong and derogatory ideas about his work, and I am afraid that the debate might get quite warm. The paper in the J. Appl. Physics is really a fraud – whether intentionally or so I can't say. But the 'Vector' maps presented in it are grossly misleading, as becomes clear when one studies the tables of data and plots the return on a map."[140] Despite the fact that Yeagley's work was so problematic, however, Griffin had little confidence that it would go away any time soon. He therefore agreed to the debate, although he warned Folk that it would likely become quite heated: "Regardless of my opinion it will not be forgotten; and its appealing simplicity has made it spread far and wide, so that one meets it at every turn. Therefore I should be glad to publicly show why I think it is so unsound, either in a two-sided debate or otherwise. But if you plan such a

[139] Donald Griffin to Harold Hitchcock, 6 December 1948, Series 1, Box 5, Folder 61, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[140] Donald Griffin to Ed Folk, 25 October 1948, Series 1, Box 3, Folder [Corr. – Folk, G. Edgar], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

show be prepared for fireworks."[141] For various logistical reasons, the debate never took place, but Griffin continued to disparage Yeagley's work any time the subject was raised.

He also took steps to prove Yeagley wrong experimentally. One of Griffin's major problems was with the "magnetic wing" experiment, which had been tried several times in the past by other ornithologists seeking to demonstrate that pigeons were sensitive to magnetism—all of this previous work yielded negative or inconclusive results, which raised serious questions about Yeagley's relatively simple experiments. And so Griffin sought the advice of behaviorist psychologist B.F. Skinner, an expert on both operant conditioning techniques and pigeon behavior.[142] In February 1948, Griffin invited Skinner to participate in a AAAS panel on bird navigation for the upcoming September meeting to discuss, among other developments, Yeagley's theory.[143] Griffin lamented that Yeagley too would be invited: "I have serious doubts about his work, but he should be heard." Griffin then explained that he was interested in conducting conditioning experiments on pigeons to see if they showed magnetic sensitivity: "This business I expect to be tedious and the results negative, but some one must do it with adequate controls to show that the birds could respond to other stimuli (visual, auditory, thermal, etc.) in the apparatus but yet could not respond to magnetic fields, static or moving."[144] Skinner was the perfect person to ask. He replied, explaining that he was

[141] Donald Griffin to Ed Folk, 25 October 1948, Series 1, Box 3, Folder [Corr. – Folk, G. Edgar], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[142] Donald Griffin to B.F. Skinner, 23 February 1948, Series 1, Box 10, Folder [Corr. – Se-Sm], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. During the war, Skinner was infamously involved in a project to develop a 'pigeon-guided missile' for the military. Dubbed "Project Pigeon," it never actually came to fruition, but it was an interesting instance in demonstrating the potential applications of operant conditioning. See C.V. Glines, "Top Secret WW II Bat and Bird Bomber Program," *Aviation History*, Vol. 15 No. 5 (2005): 38-44.
[143] The panel never materialized.
[144] Donald Griffin to B.F. Skinner, 23 February 1948, Series 1, Box 10, Folder [Corr – Se-Sm], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

impressed by Griffin's work on orientation, and that he too doubted Yeagley's findings. Furthermore, he informed Griffin about conditioning techniques that would "make it easy to discover whether pigeons are sensitive to magnetic of other forces."[145] A few years later Griffin did conduct a series of conditioning experiments, all of which yielded negative results.[146]

Within a few years, Yeagley's theory had been discredited. But it had, at least for a short time, diverted the attention of those in the field from theories based on the known senses—such as Griffin's exploratory theory—toward yet another speculative theory based on a stimulus-response mechanism. Griffin wrote to his friend Hal Hitchcock, "It makes me sick to think of all the fine birds and great effort wasted by Yeagley chasing the pot of gold at the end of the magnetic rainbow."[147] Beyond its many methodological faults and dubious assumptions, Yeagley's theory was unappealing to Griffin because it offered such a simplistic picture of bird behavior. Even though Griffin admitted that birds *might* sense magnetic and Coriolis fluctuations, those sensations would be so minor compared to their perception of more proximate and powerful stimuli that the birds almost certainly could not rely on them as orientation cues. Qualitatively, the effects might be sensible. But quantitatively, they would not register as part of the bird's general perception of its environment.[148]

---

[145] B.F. Skinner to Donald Griffin, 22 March 1948, Series 1, Box 10, Folder [Corr – Se-Sm], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[146] Donald Griffin, "Bird Navigation," *Biological Reviews*, Vol. 27 (1952): 359-390. Griffin later explained that he had in fact learned Skinner's conditioning techniques, although I do not have details of his magnetic experiments. Donald Griffin to Major Otto Meyer, 28 March 1949, Series 1, Box 7, Folder [Corr – Meyer, Otto], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[147] Donald Griffin to Harold Hitchcock, 6 December 1948, Series 1, Box 5, Folder 61, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[148] Donald Griffin, "Bird Navigation," *Biological Reviews*, p. 359-360.

Thus for Griffin, Yeagley's theory was overly tropistic: it confined bird migration and navigation to movements along physiologically determined gradients.[149] That is, rather than actively exploring their environments for visual cues, birds were simply drawn in specific directions according to inner sensations that were perhaps imperceptible as compared to their other senses.[150] Yeagley's approach, according to Griffin, relied on mechanistic assumptions that over-simplified bird behavior, and it failed to appreciate the true nature of the bird's complex relationship to the diverse features of its environment. The controversy would lead Griffin to treat magnetic theories with extreme skepticism for the rest of his career, even in the face of more legitimate evidence for magnetic perception that appeared in the 1970s.

Conclusion

Griffin's work on bird homing and migration between 1938 and 1948 had an important effect on his view of animal behavior in general. In approaching this problem, he found that one could not make sense of complex behavioral phenomena merely through the analysis of sensory mechanisms and basic environmental cues. That is, the means by which animals utilized information acquired from their surroundings was more complex than mere stimulus-response mechanisms. Instead, Griffin argued that birds seemed to perceive more holistic qualities of their environments, and utilized these complex sources of information in order to accomplish tasks for which they lacked precise physiological mechanisms. For Griffin, homing was not merely a matter of

---

[149] Donald Griffin, "Bird Navigation," *Biological Reviews*, p. 364-368.
[150] The episode affected Griffin for the rest of his career. Even as credible evidence in favor of magnetic sensibility emerged later in the 1970s, Griffin was consistently skeptical of it, to the point that he self-consciously recognized that he seemed to be the only scientist unwilling to grant the validity of mounting evidence.

external stimulation that automatically guided birds back to their home territory. Rather, it was a process of trial and error, which required that birds perceived more general environmental cues that could be used for navigation.

Griffin considered his exploratory theory of homing as a conservative interpretation of the facts. That is, he attempted to account for the homing ability in terms of the known senses, rather than the product of some mysterious or unknown sensory mechanism. He strengthened his view by drawing on Lashley's concept of instinctual behavior as that which was driven by the interaction of complex, holistic stimuli. However, this did not lead Griffin to a full explanation of homing. Some cases seemed to indicate that birds took direct paths homeward, which could not be explained merely by exploration. And while most of the data seemed to fit the theory, even his own airplane observations of homing routes could not make sense of the precise ways that birds utilized the information acquired during their apparently random wanderings.

Thus where the exploratory theory was conservative, it was also inelegant. Griffin still suspected that some piece of the puzzle was missing, but overly speculative ideas such as Yeagley's magnetic theory caused him to restrict his view to the known senses. In my next chapter, I analyze how additional work in the early 1950s showed that birds were able to use more complex sources of information—the shifting position of the sun and stars—in order to orient themselves homeward. While Griffin initially approached these findings with the same skepticism that he applied to Yeagley's theory, the solar orientation theory eventually proved to be an essential feature of bird homing and migration. These later developments would further expand Griffin's view of animal complexity, which played a crucial role in leading him to reconsider the question of animal consciousness in the 1970s.

The next chapter demonstrates how several lines of animal behavior research in the 1950s and 1960s led Griffin to expand his view of animals and their capabilities. Rather than continuing to interpret behavior through “simplicity filters,” Griffin came to realize he needed to think of animals as complex and dexterous problem solvers. Like echolocating bats, birds were also active agents that acquired and processed information from their environments, informing their daily activities. Not only was behavior flexible, at times it was seemingly the product of intelligent thought or deliberation. The ultimate outcome of this new way of thinking fully emerged in the 1970s, when Griffin proposed that animals were in fact conscious beings, capable of complex mental calculations, and that it was time to set aside behavioristic and reductionist approaches to the study of animal behavior once and for all.

CHAPTER 5
Birds, Bats, and Bees: Donald Griffin and the Emerging Picture of Animal Behavior, 1948-1970

Introduction

In this chapter I analyze Donald Griffin's professional and intellectual development during the middle decades of his career, from 1948 to 1970. During this period several new discoveries expanded his view of the complexity and versatility of animal behavior, a shift that would culminate in his subsequent investigation of animal consciousness in the 1970s. The most influential of these findings included the solar and celestial orientation of birds, the bat's use of echolocation in hunting prey, and the "dance language" of the honeybee, discovered by Austrian zoologist Karl von Frisch. Each of these discoveries surprised Griffin, and together they led him to think of animals as agents that actively utilized sophisticated sensory tools while engaging in a wide range of complex behaviors.[1] He argued that by studying the patterns of animal behavior in their natural environments, in tandem with a careful analysis of their sensory physiology, one could get a fuller and truer understanding of each. As he explained in a 1953 article on the sensory basis of orientation in birds, bats, and bees, "the baffling, almost mysterious, nature of the original phenomenon has given way to at least a partial understanding once the sensory basis was clarified…The really critical discoveries that have wholly or partly dispelled these mysteries of animal orientation have resulted from a fuller knowledge of the environmental factors actually utilized by the animals, together with new information

[1] In his historical survey of ethology, British ethologist William Homan Thorpe specified bird homing and the dance language of the honeybee as phenomena that, due to their apparent complexity, challenged zoologists and ethologists in the postwar era to rethink their relatively simple frameworks for interpreting animal behavior. William H. Thorpe, *The Origins and Rise of Ethology* (London: Praeger, 1979), p. 93-94.

about their behavioral capabilities."[2] Thus rather than restricting his view to the proximate physiological mechanisms themselves, he sought to illuminate more general features of animal behavior through the analysis of their "sensory windows" and the environmental cues mediated through those windows.[3]

Griffin also began in the immediate postwar years to establish his career as a professional scientist. Given his extensive work on animal and human physiology before and during the war, he positioned himself as a comparative physiologist in order to secure an academic job at Cornell University. He quickly learned that despite the war's end, military dollars were still flowing and could support his research on birds and bats. He consequently made strategic choices about how to frame the significance of his work more broadly in order to secure funding. His scientific output also greatly increased during the postwar period, as he published approximately seventy journal articles between 1946 and 1970. His writings also included several books and popular articles, which in addition to his well-known discovery of echolocation, significantly raised his profile in American science. His 1960 election to the National Academy of Sciences reflected the breadth of his interests and expertise, as he was appointed to both the zoology and physiology sections. Thus by the mid-1960s Griffin enjoyed the fruits of a successful academic career, and he had earned a reputation as a rigorous experimentalist and an expert on animal behavior.

Concurrent to these professional developments were significant changes in Griffin's intellectual life. Between 1948 and 1951 three major discoveries concerning the

---

[2] Donald Griffin, "Sensory Physiology and the Orientation of Animals," *American Scientist*, Vol. 41, No. 2 (Apr. 1953): 243-244.
[3] Donald Griffin, "Sensory Physiology and the Orientation of Animals," p. 244. He first introduced the "sensory window" metaphor in this 1953 article, and he frequently invoked it in several publications thereafter.

complex behaviors of birds, bats, and bees transformed his approach to animal behavior. The discoveries were significant for Griffin in two ways. First, they showed that animals—even the "lower" insects—were capable of complex behaviors such as solar orientation and symbolic communication. Thus they defied the conventional wisdom that animals were both simple and machinelike. Secondly, the concomitant frameworks for interpreting animal behavior—such as stimulus-response mechanisms and chains of associations—failed to account for these phenomena. According to Morgan's canon, scientific explanations of behavior ought to be formulated according to their lowest order of complexity, but in the case of the honeybee's dance language, for example, such explanations actually obscured the fundamental reality. The fact that these remarkable developments occurred within a short period surely intensified their influence on his scientific perspective. As a result, Griffin began to doubt that the use of "simplicity filters" were either necessary or beneficial for scientific progress. Instead, he began to think of these heuristics as harmful to scientific progress, insofar as they limited the imagination and failed to account for the complex patterns of animal behavior.

During the 1950s and 1960s, Griffin thus experienced a significant transformation in what might be called his philosophy of science. Gradually, his thinking about animal behavior became increasingly less mechanistic, insofar as those mechanisms were understood as the product of simple reactions. While the immediate causes of behavior might still be understood through the analysis of physiological mechanisms, he no longer felt compelled to reduce explanations of behavior to their simplest forms. Animals, he realized, were capable of behaviors far more complex than he had been conditioned to expect. Von Frisch's dance language theory was probably the most significant development in this regard, and the ensuing controversy in the 1960s illustrated the dangerous power of simplicity filters to inhibit the discovery of the true causes of behavior. In the remainder of this chapter I analyze how these intellectual developments, along with several professional factors, forever influenced the trajectory of Griffin's distinguished career in American biology.

Establishing a Career: From Harvard to Cornell and Back

In order to support this postwar work Griffin deployed his familiarity with the military research and funding complex that he had cultivated during his wartime projects. Throughout the 1940s and 1950s he maintained a fertile partnership with funding officers at the Office of Naval Research (ONR), and these contracts provided him with unique opportunities for animal behavior research. One such multiyear project during the summers between 1948 and 1951 brought him to the Naval Arctic Research Laboratory (NARL) in Pt. Barrow, Alaska, where he studied the physiological thermodynamics of heat insulation in mammalian fur.[4] Conducted under NARL director Laurence Irving and alongside Swedish physiologist Per Scholander, this applied research aimed to improve clothing for soldiers in extremely cold environments.[5] Griffin, however, considered it to be "pot boiler" work, particularly useful insofar as it funded his primary area of interest while in Alaska, bird migration.[6] He eventually learned that ONR was not averse to

[4] On the Naval Arctic Research Laboratory and its work, see: M.C. Shelesnyak, "Some Problems of Human Ecology in Polar Regions," *Science*, Vol. 106, No. 2757 (Oct. 1947): 405-409. A separate but related institute, the Arctic Aeromedical Laboratory in Fairbanks, focused on human physiology and medicine. See: Matthew Farish, "The Lab and the Land: Overcoming the Arctic in Alaska," *Isis*, Vol. 104, No. 1 (Mar. 2013): 1-29.

[5] This research was similar to that which Griffin conducted at the Harvard Fatigue Lab during the war.

[6] The migration and homing work in Alaska was never very successful, although while there he did develop a novel technique using radioisotopes to record the precise time that homing birds returned to their nests

funding animal navigation research outright, and so he also secured contracts to study echolocation and bird migration back home in New England.[7] His main associate at ONR was Sidney Galler, head of biology research from 1950 to 1965. Galler, who would later become the assistant Secretary of Science at the Smithsonian, was deeply interested in animal navigation, and thought that such research might yield more general insights about navigational principles useful to the military.[8] He later oversaw two of Griffin's ONR contracts in the 1950s on bat perception, which led to the significant discovery that bats use echolocation not just to navigate but also to hunt their insect prey.[9]

Substantial changes in Griffin's academic life occurred alongside these other professional developments. In 1946 he was appointed assistant professor of physiology in Cornell University's department of zoology. He leveraged his work on the sensory physiology of birds and bats, along with his wartime research on human physiology, in order to position himself as a comparative physiologist. Cornell was a good first job for Griffin. Its zoology department had a strong ornithological tradition, having maintained the Lab of Ornithology since 1915.[10] And its location in Ithaca kept him near the wild

---

during displacement experiments. Donald Griffin, "Radioactive Tagging of Animals Under Natural Conditions," *Ecology*, Vol. 33, No. 3 (Jul. 1952): 329-335.

[7] Griffin's airplane tracking of gannets in 1947 was funded by ONR, which was not particularly concerned with the research topics provided that they were conducted at the Alaska station. He justified the study of gannets in New England as a sort of 'test run' in advance of that Alaskan work. On the NARL's arctic research, see: John C. Reed and Andreas G. Ronhovde, *Arctic Laboratory: A History of the Naval Arctic Research Laboratory at Point Barrow, Alaska* (Washington, DC: ONR, 1971).

[8] Frederick Davis, *The Man Who Saved the Sea Turtles* (Oxford: Oxford University Press, 2012), p. 164.

[9] Donald Griffin, "Acoustic Location of Insect Prey by Bats," *Anatomical Record*, Vol. 111, No. 3 (1951): 448-449; Donald Griffin, "Bat Sounds under Natural Conditions with Evidence for Echolocation of Insect Prey," *Journal of Experimental Zoology*, Vol. 123, No. 3 (Aug. 1953): 435-465; Donald Griffin, Frederick A. Webster, and Charles R. Michael, "The Echolocation of Flying Insects by Bats," *Animal Behaviour*, Vol. 8, No. 3-4 (1960): 141-154; Donald Griffin and Alan D. Grinnell, "Ability of Bats to Discriminate Echoes from Louder Noise," *Science*, Vol. 128, No. 3316 (Jul. 1958): 145-147; Donald Griffin, J.H. Friend, and Frederick A. Webster, "Target Discrimination by the Echolocation of Bats," *Journal of Experimental Zoology*, Vol. 158, No. 2 (Mar. 1965): 155-168.

[10] Established by Arthur A. Allen in 1915, the Laboratory of Ornithology was the first U.S. graduate program in ornithology. It remains a prestigious research institution today.

populations of birds and bats upon which his research relied. He was thus able to continue seamlessly his work on migration and echolocation while taking on new pedagogical and professional duties.

In his teaching at Cornell Griffin applied the physiological view of biology that he had learned at Harvard in the 1930s and 1940s. As discussed in my second chapter, luminary of Harvard zoology George Howard Parker had developed a unified vision of biology that subsumed physiology, botany, and zoology under a single intellectual and administrative framework—the Institute of Biology (later known simply as the department of biology).[11] Parker and others within the department encouraged their students to view these subdisciplines as inherently integrated, based on the idea that physiological mechanisms constituted the core of functional explanations in biology. As Griffin later recalled, this philosophy led him to view physiology as a single field, "not readily divisible along phylogenetic lines."[12] Thus rather than preparing three separate courses in vertebrate, invertebrate, and general physiology, as Cornell chair of zoology Howard Adelmann initially requested, Griffin successfully argued that he ought to teach instead a single course in comparative physiology that spanned the evolutionary spectrum. Intellectually, this was consistent with his view that physiology was the common substrate of biological phenomena.[13] And pragmatically, preparing only a single course smoothed the transition from his research-oriented Harvard Junior Fellowship to

---

[11] The second chapter of my dissertation discusses this influence in greater detail.
[12] Donald Griffin, "Recollections of an Experimental Naturalist," in *Leaders in the Study of Animal Behavior*, ed. Donald Dewsbury, p. 120-142 (Cranbury, NJ: Associated Universities Press, 1985), p. 134.
[13] Beyond Griffin, the field of comparative physiology greatly expanded during the 1940s and 1950s. Much of these developments entailed experimental work on hormones and the endocrine system more broadly. On the exploration of stress physiology in endocrinology, comparative physiology, and biochemistry, see: Tulley Long, "Constituting the Stress Response: Collaborative Networks and the Elucidation of the Pituitary-Adrenal Cortical System, 1930s-1960s," (Doctoral Thesis, Johns Hopkins University, 2011).

pedagogical work at Cornell, where he immediately began teaching upon his arrival in the fall of 1946.

Due to his teaching commitments, however, the Cornell position grew cumbersome, and Griffin complained that he had increasingly less time for his own research.[14] In addition, his teaching remained in comparative physiology, but his field research continued to push him further away from laboratory approaches in physiology and toward more naturalistic studies of animal behavior in the wild. While he was primarily interested in the sensory physiology of birds and bats—particularly in its bearing on their navigation—his undergraduate and graduate teaching was restricted to large laboratory courses and small seminars on such topics as cellular physiology. Indeed, he had been hired as the zoology department's sole physiologist, and so naturally it was his responsibility to teach such courses. Griffin also privately complained about the low quality of graduate students in zoology at Cornell.[15] Although he was promoted to professor in July 1952, shortly thereafter he learned about a promising opportunity elsewhere.[16] When his uncle Alfred Redfield informed him that Harvard's biology department was seeking a new professor of zoology, Griffin jumped at the chance to return to Cambridge.[17] The teaching duties were lighter and more commensurate with his research, and as Griffin later recalled, "the stimulating environment of the Harvard Biological Laboratories and the superior facilities available at Harvard did permit better

---

[14] As he became increasingly involved with coursework at Cornell, things were also becoming busier at home. Between 1944 and 1948, he and his wife Ruth Griffin (née Castle) had four children (including twins): Nancy Griffin (b. 1943), Janet Griffin (b. 1945), and twins John Griffin and Margaret Griffin (b. 1948).
[15] Donald Griffin to George Wald, 12 January 1948, Series 1, Box 12, Folder [Corr – Wa-Whi], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[16] In 1948 Griffin was promoted to associate professor with tenure.
[17] By this point few people referred to the department as the "Institute of Biology," as G.H. Parker had.

research work than [he] would have been able to accomplish at Cornell."[18] Immediately upon returning to Harvard, he began teaching an advanced course on the physiological basis of animal behavior—clearly a move away from his Cornell teaching, and toward topics more relevant to his own research.[19]

Evidently Harvard's chair of biology at the time, Frank M. Carpenter (1902-1994), construed Griffin's role as a professor of animal behavior more generally.[20] Carpenter, a former student of William Morton Wheeler, was more focused on the museum side of biology, and lacked the physiological orientation of his predecessors in the biology chair. He hoped that Griffin, unlike Lashley in the 1930s, would make strong interdisciplinary connections between Harvard's biology and psychology departments.[21] Doyen of American psychology E.G. Boring was also sanguine about the appointment, writing to Griffin: "So many times I have wanted to write you to tell you how welcome you would be at Harvard among the people in our Department and among the biologists whom I know…And of course our whole Department has felt that this was the best appointment Biology had made in the history of anyone here…I hope it can be worked to bring certain sensible liasons [sic] between the two departments where there is natural overlap."[22] Lashley too thought Griffin was a great fit at Harvard, having recommended

[18] Donald Griffin, "Recollections of an Experimental Naturalist," p. 139.
[19] Donald Griffin to Howard Adelmann, 15 October 1955, Series 1, Box 2, Folder [Unnumbered], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[20] Frank Carpenter was chair from 1952-1959.
[21] In fact, Griffin's doctoral advisor Karl Lashley had been jointly appointed to the departments of biology and psychology for the same reason, although he was largely unsuccessful in creating interdisciplinary connections. Several interdepartmental squabbles eventually led Lashley to leave Harvard for the Yerkes Laboratories of Primate Biology in 1942. See Nadine Weidman, *Constructing Scientific Psychology: Karl Lashley's Mind-Brain Debates* (Cambridge: Cambridge University Press, 2006), p. 143-154.
[22] Edwin G. Boring to Donald Griffin, 4 February 1953, Series 1, Box 1, Folder [Corr. Bi-Bo], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. Boring's views on the importance of interdisciplinary work in biology and psychology were consistent with Harvard's 1945 report on the future of psychology in the American university. See: *The Place of Psychology in an Ideal University* (Cambridge: Harvard University Press, 1947), p. 20-23.

him earlier in 1951 for another position.[23] According to Lashley, there was "no other young biologist who equals him in range of interest in animal behavior, in experience in devising experimental controls in field studies, and in the energy and enthusiasm with which he carries his work." Among those at the top of the field in animal behavior, Lashley continued, "Griffin is by far the ablest in breadth of interest and grasp of problems."[24] These lofty expectations proved correct, as Griffin would go on to a successful career in the biology department, where he eventually served as chair of zoology from 1963 to 1965. He also formed institutional and intellectual bridges between the biology and psychology departments, serving on the latter's hiring committee throughout the 1950s.[25]

Griffin's appointment in the biology department, along with the promise of his contributions to interdisciplinary science, were consistent with a larger trend at Harvard in the early 1950s. As recommended by the famous 1945 report, *General Education in a Free Society*, Harvard pedagogy in the postwar period began to shift from a tradition of specialization toward a more generalist character, which emphasized synthetic research and the formalization of interdisciplinary bodies.[26] The report recommended that the sciences, and in particular introductory courses therein, ought to forgo overspecialization and emphasize instead general principles and "broad syntheses" in order to meet the

---

[23] In this earlier episode, Lashley recommended Griffin for a new Agassiz professorship in the Museum of Comparative Zoology (MCZ). That position instead went to Ernst Mayr of the American Museum of Natural History, who was evidently thought to be better suited for museum work than Griffin. Mayr would become director of the MCZ upon Alfred Romer's retirement in 1961.
[24] Karl Lashley to Alfred Redfield, 18 April 1951, Series 1, Box 9, Folder [Corr. Ra-Ri], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[25] Nathan Pusey to Donald Griffin, 24 March 1954, Series 1, Box 10, Folder [Corr. – Personal, Harvard University], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[26] *General Education in a Free Society* (Cambridge: Harvard University Press, 1945), p. 221. On interdisciplinarity within the "Harvard complex," see: Joel Isaac, *Working Knowledge: Making the Human Sciences from Parsons to Kuhn* (Cambridge: Harvard University Press, 2012).

demands of a changing intellectual landscape. Provost of Arts and Sciences Paul H. Buck, who chaired the "Committee on the Objectives of a General Education in a Free Society," similarly saw Griffin as a promising contributor to this new vision of science at Harvard.[27] Griffin's work on animal behavior, sensory physiology, and perception reflected such a synthetic approach to solving biological problems, and thus institutional leaders such as Buck, Boring, Lashley, and Carpenter saw his work as embodying that interdisciplinary ideal.

Griffin returned to Harvard in the summer of 1953 as a tenured professor of zoology, bringing with him several ONR contracts for research on bird and bat navigation.[28] This was an important year not just for his professional, but for his intellectual life as well, as several key developments in the early 1950s led him to think about his work more broadly. As we have seen, he was particularly focused on animal navigation, an interest that was catalyzed not only by his discovery of echolocation, but by Karl von Frisch's theory of the honeybee "dance language." Griffin considered the study of navigation as an important means to investigate more general features of animal behavior such as its psychological, evolutionary, and ecological dimensions. For example, the discovery of echolocation in marine mammals and cave-dwelling birds indicated that one could study comparatively the relationship between behavior and perception by examining how different species employed their sensory modalities in a variety of environments and behavioral contexts. He also began an extensive comparative

[27] Professor of zoology and Associate Dean of Arts and Sciences Leigh Hoadley was also on the committee that made these recommendations, which was chaired by Paul H. Buck, the Dean of Arts and Sciences at Harvard. Buck happily recommended Griffin as the department's choice to the Harvard Corporation, who similarly approved of the appointment. Paul H. Buck to Donald Griffin, 20 November 1952, Series 1, Box 5, Folder 58, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

[28] F.M. Carpenter to Donald Griffin, 24 October 1952, Series 1, Box 5, Folder 58, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

study of echolocation in different genera and species of bats, analyzing how environmental and behavioral factors led to differences in the biophysical properties of their ultrasonic signals.[29] Thus while Griffin continued to focus on the sensory basis of animal perception, he also began to inquire about broader features of their behavior. This entailed searching for evolutionary explanations for the development of different modes of perception, and more detailed inquiry into the environmental factors utilized in the behavioral patterns of various animals.[30]

The shift toward a more general study of animal behavior also paralleled the expansion of European ethology, with which Griffin became increasingly familiar due to the proliferation of international journals and conferences in the postwar years.[31] The intellectual maturation of ethology in this period, most notably characterized by the work of Niko Tinbergen and Konrad Lorenz, focused on the study of instincts in wild populations (Tinbergen) and freely-ranging domesticated species (Lorenz).[32] Although its

---

[29] On these comparative studies, see for example: Donald Griffin, "High Frequency Sounds of Tropical Bats," *Anatomical Record*, Vol. 117 (1953): 567; Alan Grinnell and Donald Griffin "The Sensitivity of Echolocation in Bats," *Biological Bulletin*, Vol. 114, No. 1 (Feb. 1958): 10-22; Donald Griffin, A. Novick, and M. Kornfield, "The Sensitivity of Echolocation in the Fruit Bat, Rousettus," *Biological Bulletin*, Vol. 115, No. 1 (Aug. 1958): 107-113**;** Donald Griffin, *Listening in the Dark*: *The Acoustic Orientation of Bats and Man* (New Haven: Yale University Press, 1958), p. 203-255.

[30] For example, Griffin became interested in echolocation in porpoises and bottlenose dolphins after Winthrop N. Kellogg made this discovery in the early 1950s: W.N. Kellogg, Robert Kohler, and H.N. Morris, "Porpoise Sounds as Sonar Signals," *Science*, Vol. 117, No. 3036 (Mar. 1953): 239-243; Donald Griffin, "Hearing and Acoustic Orientation in Marine Animals," *Deep-Sea Research*, Vol. 3 (1953): 406-417.

[31] On the more general postwar influence of European ethology on the study of animal behavior in the U.S., see: Richard Burkhardt, *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology* (Chicago: University of Chicago Press, 2005), especially chapters five through seven; Donald Dewsbury, "A Brief History of the Study of Animal Behavior in North America," in *Perspectives in Ethology*, Vol. 8, eds. P.P.G. Bateson and P.H. Klopfer, p. 85-122 (New York: Plenum, 1989), p. 110-114; Donald Dewsbury, "Americans in Europe: The Role of Travel in the Spread of European Ethology after World War II," *Animal Behaviour*, Vol. 49 (1995): 1649-1663.

[32] Burkhardt characterizes Tinbergen, who was more keen to study wild animals in their natural habitats, as the "hunter," as opposed to Lorenz, the "farmer," who worked mainly with domesticated animals. On Lorenz's theory of instinctive behavior, see: W.H. Thorpe, *The Origins and Rise of Ethology: The Science of the Natural Behavior of Animals* (New York: Praeger, 1979), p. 87-107; Richard Burkhardt, *Patterns of Behavior*, p. 127-186.

theoretical components were largely ignored by behavioral scientists across the Atlantic, many ideas and discoveries generated by European approaches became more extensively known in the United States in the late 1940s and 1950s.[33] And in fact Griffin's popularization of Karl von Frisch's work contributed to the increasing familiarity with European inquiry on animal behavior. These ethological approaches, however, stood in rather stark contrast to much of the work on animal behavior conducted by American comparative psychologists, who were primarily interested in the laboratory analysis of learning and conditioning in domesticated animals such as the white rat.[34] Like comparative psychology, however, European ethology was also largely behavioristic vis-à-vis questions about animal subjectivity. For Tinbergen and Lorenz, the seeming impossibility of objectively studying animal minds rendered such mentalistic categories useless in analyzing the causes of behavior.[35] While he never embraced the theoretical contributions of ethology, Griffin's work on the naturalistic behavior of wild birds and bats nevertheless had more in common with his European counterparts than with the main currents of American work on animal behavior.

In the remainder of this chapter I analyze three major developments in the 1950s that profoundly altered Griffin's understanding of animal behavior. The first of these was

---

[33] Konrad Lorenz's theoretical constructs such as innate releasing mechanisms and the psychohydraulic model of motivation, for example, did not find a receptive audience among comparative psychologists studying animal behavior. On the American critical reaction to ethology, especially psychologist Daniel Lehrman's acclaimed 1953 critique of Lorenz's theory, see: Richard Burkhardt, *Patterns of Behavior*, p. 384-390; Daniel Lehrman, "A Critique of Konrad Lorenz's Theory of Instinctive Behavior," *The Quarterly Review of Biology*, Vol. 28, No. 4 (Dec. 1953): 337-363.

[34] W.H. Thorpe, *The Origins and Rise of Ethology*, p. 94-96; Richard Burkhardt, "On the Emergence of Ethology as a Scientific Discipline," *Conspectus of History*, Vol. 1, No. 7 (1981): 73; Donald Dewsbury, "Americans in Europe: The Role of Travel in the Spread of European Ethology after World War II," *Animal Behaviour*, Vol. 49 (1995): 1649-1663.

[35] Gordon Burghardt, "Animal Awareness: Current Perceptions and Historical Perspective," *American Psychologist*, Vol. 40, No. 8 (Aug. 1985): 909. In fact Lorenz thought that subjectivity was an important feature in driving the appetitive behavior of animals, although he was unwilling to make any strong claims about the nature of such subjective desires.

Karl von Frisch's theory of the "dance language" of honeybees, a famous discovery for which he eventually shared the 1973 Nobel Prize in Physiology or Medicine. As Griffin later recalled, von Frisch's discovery was a "startling development" that "shook up [his] whole scientific viewpoint."[36] Complementing that breakthrough were further surprises in the field of bird homing and migration. As of 1950, Griffin had yet to identify a physiological 'smoking gun' that accounted for the ability of birds to orient themselves homeward from unfamiliar territory. As we have seen in the previous chapter, this led him to opt for what he considered the most parsimonious explanation, which held that birds scattered randomly and only found their way home when they chanced upon familiar territory recognizable from previous flights.[37] In the early 1950s, new research subverted his exploratory theory by showing that birds oriented themselves based on information gleaned from the motion of the sun—a method that he had tentatively considered but never seriously examined. German ornithologist Gustav Kramer and British ornithologist G.V.T. Matthews conducted the most important research on this novel theory of orientation. The theory gained further credibility from von Frisch's demonstration that bees, thought to be vastly simpler in their behavior and neurophysiology than birds, were nonetheless capable of solar orientation.[38] And finally, Griffin's own research on bats yielded more surprises about the versatility of their behavior and the refinement of echolocation. He was stunned to find that bats used echolocation not merely for basic functions such as avoiding obstacles or finding the

---

[36] Donald Griffin, "Recollections of an Experimental Naturalist," p. 135-136.
[37] As I show in the previous chapter, most experts in ornithology agreed with Griffin's interpretation.
[38] Griffin explained to von Frisch, "This point of view [of sun orientation in birds] is certainly more attractive after your evidence showing the complex and precise use made of the sun's bearing by bees." Donald Griffin to Karl von Frisch, 8 May 1948, Series 1, Box 11, Folder 105, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

entrances to their caves, but for the seemingly complex feat of hunting insects on the wing. He also later found that their target discrimination was extremely precise, and that the high signal-to-noise ratio of their echolocation had significant implications for understanding various additional features of their behavior. These new insights partially resulted from moving his study of bats from the laboratory into their natural habitats, where he was uniquely able to analyze their hunting behavior.

For Griffin, the impact of the whole of these discoveries was greater than their sum, and together they caused him to broaden his understanding of the complexity of animal behavior. They also led him to dismiss the utility of applying "simplicity filters," such as his exploratory theory of bird navigation, which restricted scientific explanations of behavior to their lowest order of complexity. And most significantly, this changed perspective opened the possibility for Griffin to explore new questions about animal cognition and consciousness in the later decades of his career.

Karl von Frisch and the "Dance Language" of the Honeybee

Austrian zoologist Karl von Frisch (1886-1982) spent a long, illustrious career studying the sensory physiology and behavior of bees and fish.[39] In a long series of experiments beginning in the 1910s and culminating in the 1940s, he famously discovered that honeybees communicated precise information about the location of nectar

---

[39] On von Frisch's life and work, see Tania Munz's recent work: Tania Munz, "Of Birds and Bees: Karl von Frisch, Konrad Lorenz, and the Science of Animals, 1908-1973," (Doctoral Thesis, Princeton University, 2007); Tania Munz, "The Bee Battles: Karl von Frisch, Adrian Wenner and the Honey Bee Dance Language Controversy," *Journal of the History of Biology*, Vol. 38 (2005): 535-570. Von Frisch self-identified as a physiologist rather than an ethologist, but Munz has argued for his inclusion as a significant contributor to the development of professional ethology.

sources to one another using what he characterized as a "dance language."[40] He also found that bees could perceive ultraviolet radiation and the polarization of sunlight across the sky, and that this allowed them to determine the sun's position for the purpose of orientation in adverse visual conditions. According to historian of science Richard Burkhardt, von Frisch's "remarkable discovery of the dance 'language' of the honeybee is generally regarded by ethologists as the single most important contribution to the study of animal behavior of the twentieth century."[41] The dance language theory was both shocking and controversial, as it challenged the view that symbolic language was the exclusive provenance of human beings. Whereas it was widely accepted that invertebrates were capable of communication via mechanisms such as chemical signaling, von Frisch's theory suggested that bees possessed a language, which seemed to indicate a far more complex neurophysiological basis for that communicative behavior. The discovery was also surprising because it demonstrated that the information transmitted via the honeybee language was not only abstract, but also impressively precise, indicating both the direction and distance of nectar sources.

As historian Tania Munz has explained, von Frisch's theory sparked a heated controversy in the late-1960s that centered on the question of whether bees actually utilized the information encoded in their dances in order to locate nectar.[42] On one side of this debate were von Frisch, Donald Griffin, and other zoologists who were impressed by the complexity and versatility of animal behavior as demonstrated by the symbolic

---

[40] Von Frisch first published his "dance language" theory in 1946: Karl von Frisch, "Die 'Sprache' der Bienen und ihre Nutzanwendung in der Landwirtschaft," *Experientia*, Vol. 2, No. 10 (1946): 397-404. See also: Karl von Frisch, *Bees: Their Vision, Chemical Senses, and Language* (Ithaca: Cornell University Press, 1950).

[41] Richard Burkhardt, "Karl Ritter von Frisch," *Complete Dictionary of Scientific Biography*, Vol. 17 (Detroit: Charles Scribner's Sons, 2008), p. 312.

[42] Tania Munz, "The Bee Battles," *Journal of the History of Biology*, Vol. 38 (2005): 535-570.

communication system of bees. Opposed to this view were biologist Adrian Wenner and his behaviorist colleagues, who charged that the behavior in question could be more simply explained via olfaction, and that the linguistic elements of the theory rendered it unnecessarily complex.[43] Wenner and his colleagues explained that although their experiments on olfaction had not disproved the dance language theory, they offered "a more simple interpretation" of the results.[44] Their opposition was thus a quintessential application of Lloyd Morgan's canon, a philosophical variant of Ockham's razor intended to restrict explanations of animal behavior to their lowest order of psychic complexity.[45] Eventually the debate was settled in favor of von Frisch, whose victory culminated in his reception of the 1973 Nobel Prize in Physiology or Medicine (along with Konrad Lorenz and Niko Tinbergen for their own contributions to ethology).[46]

Since von Frisch's discovery of the dance language is a classic story in the history of ethology, I will only briefly recount it in broad strokes.[47] Beginning around 1920, his observations of the social behavior of honeybees seemed to indicate that they conveyed to one another the location of nectar and pollen sources through some indeterminate communicative mechanism. He observed that foraging bees performed a ritualistic "dance" when returning to the hive from a profitable source of nectar or pollen, and that

[43] As Munz has described, Wenner took a particularly mathematical approach to biological problems, which led to both disagreements and confusion in his debates with von Frisch and his supporters.
[44] Karl von Frisch, Adrian Wenner, and Dennis Johnson, "Honeybees: Do They Use Direction and Distance Information Provided by Their Dancers," *Science*, Vol. 158 (1973): 1077.
[45] On Morgan's purpose for formulating the canon, and how subsequent scientists and historians have misinterpreted his intentions, see: Alan Costall, "How Lloyd Morgan's Canon Backfired," *Journal of the History of the Behavioral Sciences*, Vol. 28 (Apr. 1993): 113-122. Griffin eventually coined the derogatory term "simplicity filters" for such heuristics, which he criticized for unduly restricting scientific creativity and for obscuring accurate interpretations of complex behavior.
[46] On the history of ethology and the significance of the 1973 Nobel Prize, see: Richard Burkhardt, *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology* (Chicago: University of Chicago Press, 2005), especially chapter ten.
[47] The definitive source on von Frisch's discovery is Tania Munz's dissertation (unpublished): Tania Munz, "Of Birds and Bees: Karl von Frisch, Konrad Lorenz, and the Science of Animals, 1908-1973," (Doctoral Thesis, Princeton University, 2007).

after mimicking the dance, other bees departed the hive and invariably discovered the source. For several decades von Frisch suspected that the bees' highly refined olfactory sense was probably responsible: thus when a forager returned to the hive, other bees detected trace elements of the specific nectar or pollen lingering on the forager's antennae, and they used their olfactory sense to locate its origin.[48] Just after the war in the summer of 1945, however, von Frisch began analyzing the dance's finer movements, which ultimately led to his famous discovery.[49]

In these later experiments, von Frisch observed that the dance patterns varied according to the distance between the hive and the nectar or pollen sources.[50] Bees performed the first type—the "Rundtanz" (round dance)—when returning from a source that was relatively close to the hive. In such cases, von Frisch concluded, olfactory cues constituted the primary mechanism by which other bees located the nectar sources; thus the forager's round dance merely indicated that it had located a source relatively close to the hive, and other bees were stimulated by the dance to leave the hive in search of that nectar via olfaction. And when sources of nectar were richer and in greater supply, the foraging bees danced more vigorously in order to convince more of their brethren to seek out the prize.

As the distance to the nectar increased beyond 50 meters, however, the round dance gradually gave way to another style. And at distances greater than 100 meters, the bees performed this other dance exclusively. Von Frisch termed the second dance the

---

[48] He also thought that the type of dance performed by the bees distinguished nectar from pollen sources.
[49] During the war von Frisch was commissioned by the Nazi regime to conduct applied research on pollination in the hopes of improving German agriculture. As Tania Munz has shown, von Frisch framed his work as useful to the state, although he opposed Nazi sociopolitical ideologies: Tania Munz, "Of Birds and Bees," p. 106-149.
[50] Henceforth I will simply say nectar source, although von Frisch found that the dances also indicate sources of pollen and other objects of biological significance.

“Schwänzeltanz” (tail waggle or wagging dance), which entailed the repetition of a “straight run” movement followed by a figure-eight pattern, in which the bees vigorously waggled their abdomens on the surface of the honeycomb.[51] He found that the straight run indicated the direction of the nectar source, but because the honeycomb is typically oriented vertically, bees transposed the horizontal direction of the nectar onto the vertical plane of the honeycomb. In order to do this, they utilized information about the location of the nectar source relative to the position of the sun. For example, if the nectar was twenty degrees to the right of the sun’s direction, then the straight run of the dance was 20 degrees to the right of the vertical axis of the honeycomb. Von Frisch would later discover in 1948 that even when the sun was partially obscured by clouds, bees were able to determine its absolute position by sensing the polarization of light in the blue sky.[52] Remarkably, the dance also indicated the distance between the nectar source and the hive.[53] This information was encoded by the frequency of the waggles in the figure-eight motion: more waggling indicated that the source was close to the hive, and less waggling indicated a greater distance.[54] In addition, von Frisch found that the dances constituted a versatile language, as bees also used it to communicate the locations of other biologically significant resources such as potential hive sites and water.

Upon learning about von Frisch’s work in the spring of 1948, Griffin became a champion of the dance language theory in the United States. Although he was initially

[51] He had discovered the waggle dance several decades before, but thought that it was used to designate pollen sources exclusively, whereas the round dance was thought to signify nectar. It was not until the crucial experiments of 1945 that he realized the true significance of the waggle dance.
[52] In addition, since ultraviolet radiation more readily penetrates cloud cover than visible light, the bee’s ability to perceive UV light aided them in determining the precise position of the sun.
[53] The distance was given in terms of the time it took the bee to fly from the hive to the source, rather than in absolute spatial terms.
[54] Karl von Frisch, *Bees*, p. 78. The distance was indicated not by its spatial position, but by the approximate time that it took the bees to fly from the hive to the nectar.

skeptical, he became satisfied with its general validity after successfully repeating several of the experiments at Cornell. For Griffin, who was "so fascinated by this revolutionary discovery," the dance language theory had important implications about animals in general. For one, it indicated that lower animals were capable of exhibiting a type of symbolic language, which up to that point had been thought to be the exclusive provenance of human beings. As Tania Munz has emphasized, however, von Frisch was never quite comfortable comparing the dance language to human language, and in fact he typically wrote "language" in quotation marks in order to deflect charges that he was anthropomorphizing the phenomenon.[55]

Regardless of its resemblance to human language, however, the bee dances obviously constituted a complex mode of communication insofar as they involved encoding abstract information about distance and direction into a coordinated system of physical gestures. But Griffin was also impressed by the complexity of the orientation behavior that undergirded the communications of bees. The fact that bees were able to determine the precise location of nectar sources relative to that of their hive and to the changing position of the sun was stunning; it implied that bees had a highly developed perception of time and space, and that they were able to encode spatial information onto a kind of cognitive map that led to distant goals. As he explained at the time of the discovery, "The 'language' of bees does not employ words or even sounds, but serves nonetheless to convey complex information, and even seems to involve something

---

[55] During mid-twentieth century work on animal behavior, to be accused of anthropomorphism was a serious indictment of the integrity and validity of one's work, and von Frisch certainly wished to avoid that charge. See: John S. Kennedy, *The New Anthropomorphism* (Cambridge: Cambridge University Press, 1992), p. 1-7; *Anthropomorphism, Anecdotes, and Animals*, eds. Robert Mitchell, Nicholas Thompson, and H. Lyn Miles (Albany: SUNY Press, 1997), especially chapters 1, 11, and 16.

analogous to map reading."[56] For ten years Griffin had been trying to solve the problem of bird migration from within a mechanistic framework, searching for the environmental cues utilized in orientation. In the dance language of the honeybee, he found evidence that the mechanisms of animal orientation could be far more complex than the mere perception of environmental stimuli. Rather, it showed that animals were able to do something akin to rudimentary information processing, as they made calculations about direction and distance, and utilized a system of communicative gestures to encode and transmit that information to other individuals.

So impressed was Griffin that he invited von Frisch to present his work at a special symposium on animal navigation that Griffin was planning for the 1948 AAAS meeting in Washington, DC. Due to financial difficulties and postwar travel restrictions, however, he was unable to commit in such short order, and so Griffin arranged for von Frisch's former student Ernst Wolf, to present instead.[57] In the meantime, Griffin began arranging a larger-scale lecture tour for von Frisch across several universities in the United States and Canada.[58] To finance the trip, he turned to the Rockefeller Foundation, which had become a leading source of support for such international exchanges in the years following the war.[59] And to help persuade the Foundation to support the trip, Griffin asked the esteemed Danish physiologist and Nobel laureate August Krogh (1874-1949) to write a letter of support, which helpfully explained the unpopularity of von

---

[56] Donald Griffin, forward to *Bees: Their Vision, Chemical Senses, and Language*, by Karl von Frisch (Ithaca: Cornell University Press, 1950), v-ix.
[57] At the time Austrian zoologist Ernst Wolf was a professor at Wellesley College. The symposium, "Mechanisms of Animal Migration and Homing," was held at the AAAS meeting on September 13-17, 1948, in Washington, DC.
[58] Donald Griffin, "Recollections of an Experimental Naturalist," p. 135-137.
[59] Janet Paine, who oversaw Rockefeller's German and Austrian exchanges, was Griffin's primary contact.

Frisch's work with Nazi officials.[60] The Rockefeller Foundation ultimately agreed to finance $2100 for the trip on the condition that other institutions matched their funding.[61] Griffin therefore began a mad scramble to secure funds and commitments from other universities for a months-long journey in the spring of 1949. The trip was largely successful, and von Frisch presented his work in various formats at several top universities.[62]

In his efforts to popularize the discovery, Griffin also edited and oversaw the publication of von Frisch's lectures in a short book, *Bees: Their Vision, Chemical Senses, and Language*, published in English by Cornell University Press in 1950.[63] In the forward, Griffin mused about the profound implications of the dance language theory, arguing that its "wholehearted acceptance involves a considerable revision of current scientific attitudes."[64] He further suggested that the discovery validated questions about the "higher mental faculties" involved in the behavior of lower animals, which had been rejected as unscientific in the heyday of behavioristic and mechanistic approaches to behavior: "In recent decades biologists have grown reluctant to credit any claim that the reactions of lower animals attain a high degree of complexity, or what one might be tempted to call intelligence." He concluded that the "truly revolutionary" character of von

---

[60] Donald Griffin to August Krogh, 17 September 1948, Series 1, Box 11, Folder 105, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. As Tania Munz has shown, von Frisch had been unfairly accused of cruelty to animals in the early 1930s, which rather ironically drew the ire of Nazi officials. Tania Munz, "Of Birds and Bees," p. 106-108.

[61] Evidently this was a standard practice of the Rockefeller Foundation when supporting such trips. Donald Griffin to Karl Lashley, 21 December 1948, Series 1, Box 6, Folder 73, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

[62] The trip included stops at universities such as Cornell, Yale, Harvard, and the University of Chicago. In addition, von Frisch presented at the U.S. Department of Agriculture in Washington, DC, and made a trip to the Yerkes Primate Laboratories in Orange Park, Florida, where he was hosted by Karl Lashley.

[63] Karl von Frisch, *Bees: Their Vision, Chemical Senses, and Language* (Ithaca: Cornell University Press, 1950).

[64] Donald Griffin, forward to *Bees: Their Vision, Chemical Senses, and Language*, by Karl von Frisch (Ithaca: Cornell University Press, 1950), vii.

Frisch's findings ought to lead scientists to "readjust our thinking about animal behavior in the light of these findings and the implications that flow from them."[65]

In a similarly provocative article on von Frisch's theory, August Krogh explained: "I would ask you to give some thought also to the mind of the bees. I have no doubt that some will attempt to 'explain' the performances of the bees as the result of reflexes and instincts. Such attempts will certainly contribute to our understanding, but for my part I find it difficult to assume that such perfection and flexibility in behavior can be reached without some kind of mental processes going on in the small heads of the bees."[66] But not every scientist agreed with Krogh and Griffin. In his review of von Frisch's book, American comparative psychologist T.C. Schneirla considered it "unfortunate that the Foreword offers a vague psychological interpretation which goes considerably beyond the evidence."[67] For Schneirla, years of study on conditioning and learning in insects had convinced him that behavioral complexity did not imply intelligence in its "higher-level sense," since seemingly complex behaviors could result from basic conditioning and without explanations that invoked higher psychological faculties.[68] Schneirla's view found its ultimate manifestation in Adrian Wenner's stimulus-response framework for explaining the nectar seeking behavior of bees, which incited the aforementioned scientific controversy in the late 1960s.[69]

Griffin, however, was uninterested in laboratory conditioning approaches to the general understanding of behavior, and instead focused on the sensory basis of the natural

---

[65] Donald Griffin, forward to *Bees: Their Vision, Chemical Senses, and Language*, by Karl von Frisch (Ithaca: Cornell University Press, 1950), viii.
[66] August Krogh, "The Language of the Bees," *Scientific American*, Vol. 179 (Aug. 1948): 18-21.
[67] T.C. Schneirla, "Bees," *Ecology*, Vol. 32, No. 3 (Jul. 1951): 565.
[68] Schneirla spent several decades working on insect learning at the American Museum of Natural History in New York. He and Griffin knew each other well, although their work rarely overlapped.
[69] Tania Munz, "The Bee Battles: Karl von Frisch, Adrian Wenner and the Honey Bee Dance Language Controversy," *Journal of the History of Biology*, Vol. 38 (2005): 535-570.

behavior of animals. While conditioning techniques were useful insofar as they revealed the physical limits of sensation (the presence or absence of magnetic sensitivity, for example), he did not view this as the key to understanding behavior. For him, von Frisch's discovery firmly demonstrated that the lower organisms were capable of truly complex behavior, as it defied explanation from within a simple stimulus-response framework. And eventually the predictions set forth in his forward proved correct. As ethologist James L. Gould, a graduate student of Griffin's whose work served as the conclusive confirmation of von Frisch's theory, explained in 1975:

> Some of the resistance to the idea that honey bees possess a symbolic language seems to have arisen from a conviction that "lower" animals, and insects in particular, are too small and phylogenetically remote to be capable of "complex" behavior. There is perhaps a feeling of incongruity in that the honey bee language is symbolic and abstract, and, in terms of information capacity at least, second only to human language. Despite expectations, however, animals continue to be more complex than had been thought, or than experimenters may have been prepared to discover. Especially in ethology, it is difficult to avoid the unprofitable extremes of blinding skepticism and crippling romanticism.[70]

Despite the relatively cold response from skeptics such as Schneirla and Wenner, most scientists eventually came to recognize that von Frisch's discovery had fundamentally recast the question of intelligent behavior in lower animals. And this view was crystallized further when the theory was sanctified with the 1973 Nobel Prize, thus ending the Wenner controversy for all intents and purposes.[71]

In his autobiographical memoir of 1985, Griffin would later recall that von Frisch's work subverted the Loebian conception of animal navigation: "Good god, if mere insects communicate abstract information about distance and direction, where does

[70] James L. Gould, "Honey Bee Recruitment: The Dance-Language Controversy," *Science*, Vol. 189, No. 4204 (Aug. 1975): 692. Gould's assessment of the controversy thus mirrors that of his advisor and mentor, Griffin.
[71] In fact the controversy dragged on for a few more years, but by the mid-1970s Wenner found himself increasingly isolated in his opposition.

that leave Loebian tropisms?"[72] This sentiment, however, is somewhat disingenuous. Hardly any zoologist at the time would have invoked Loeb's turn-of-the-century framework to explain the orientation of invertebrates, and there is no evidence that Griffin's understanding of phenomena such as echolocation or bird navigation relied on such mechanisms.[73] By 1950 the cachet of Loebian tropisms had long been surpassed by the work of physiologists such as Gottfried Fraenkel and Donald L. Gunn, who theorized a more elaborate scheme of "taxes" and "kineses" to understand and categorize a wider range of locomotion and modes of orientation.[74] To be fair, Griffin mentions elsewhere in the essay that perhaps his ideas were more in line with those of Fraenkel and Gunn.[75] In that framework, however, animal orientation was still understood as the product of mechanistic reactions, although it was far more elaborate than Loeb's theory.[76] What Griffin's rhetoric really captures is the idea that animal navigation at the time was understood in simple, stimulus-response terms, which was certainly in keeping with Loeb's mechanistic view of biology.[77] And it was precisely the revision of this type of reductionist formulation that he predicted would result from a proper understanding of the "dance language" and its greater implications.

---

[72] Donald Griffin, "Recollections of an Experimental Naturalist," p. 136. Griffin repeated this rhetorical question in another autobiographical essay: Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography,* Vol. 2, ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 79.

[73] In fact, he was openly critical of Yeagley's magnetic orientation theory because its tropistic simplicity was reminiscent of Loebian orientation in lower animals (see previous chapter).

[74] Gottfried Fraenkel and Donald Gunn, *The Orientation of Animals: Kineses, Taxes, and Compass Reactions* (Oxford: Oxford University Press, 1940).

[75] Donald Griffin, "Recollections of an Experimental Naturalist," p. 135.

[76] On Loeb's theory of orientation and his debate with Herbert Spencer Jennings in the early-twentieth century, see: Philip J. Pauly, "The Loeb-Jennings Debate and the Science of Animal Behavior," *Journal of the History of the Behavioral Sciences*, Vol. 17 (1981): 504-515.

[77] On Loeb's mechanistic vision of biology, see: Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (Oxford: Oxford University Press, 1987).

For Griffin, von Frisch's theory revealed that animal behavior—even in the lower invertebrates—could be far more complex than that for which extant frameworks allowed. More specifically, it suggested that in order to understand how animals accomplish difficult tasks such as homing, one might have to seek explanations well beyond the type of basic sensory mechanisms for which Griffin had been searching. Beyond that, it signified that the use of "simplicity filters," which restricted scientific explanations to their most parsimonious formulations, might actually inhibit rather than improve scientific inquiry. This revelation came at an important moment in Griffin's own research on bird homing and migration, since he had for several years affirmed that the most conservative interpretation of his data was that birds utilized a simple and random exploratory method. Von Frisch's work demonstrated that bees were able to perceive polarized light, to track the shifting position of the sun, to make calculations about distance and direction, and to encode such information for the purpose of communication. If bees could perform such complex feats, what might birds be doing when homing? Could the parsimonious theory of random exploration be obscuring a more fundamental understanding of birds and their behavior? At around the same time several new developments in the field of bird migration revealed that this behavioral ability was indeed far more complex than Griffin and others suspected, and this new knowledge further expanded his view of the complexity and versatility of animal behavior.

Birds Do It Too: The Solar Theory of Orientation

As was discussed in chapter four, Yeagley's magnetic theory proposed in 1947 generated much controversy and criticism, and failed to persuade Griffin because of serious flaws in his experimental methods. But new work that followed soon after the Yeagley controversy reopened the question of navigation via specific environmental cues, and had the opposite effect on Griffin, causing him to take these more complex mechanisms seriously. In the late 1940s, his exploratory theory was the most widely accepted explanation among American biologists, although it was hardly comprehensive or satisfying. Essentially, Griffin held that birds navigated homeward merely as the result of encountering by chance territory that was already familiar to them. In the early 1950s, however, several important discoveries were made across the Atlantic, significantly altering the terrain. As the result of this work, scientists came to realize that birds were capable of navigation by utilizing much more complex sources of information gleaned from their environments.

A major breakthrough in the study of bird migration occurred around 1950, when British ornithologist Geoffrey V.T. Matthews (1923-2013) and German ornithologist Gustav Kramer (1891-1957) developed the solar orientation (or "sun arc") theory of bird navigation. Through a series of clever experiments, Matthews showed that pigeons and Manx shearwaters used the sun's shifting position across the sky to orient themselves in the direction of their goals. The theory held that these birds accounted for the sun's position at the "local" time of the territory that they wished to reach, and compared that position with the relative trajectory of the sun in unfamiliar territory. Thus the sun arc theory relied on recent theoretical work on what came to be known as the "biological clock," a concept that was becoming increasingly important in physiology during the

1950s.[78] Kramer, who studied the natural migrations of birds, also contributed to the theory of solar orientation through his laboratory investigation of starlings.

Although the sun arc theory was not a comprehensive or universal explanation of bird migration, it solved several major problems of orientation and took by surprise skeptics such as Griffin. And much like von Frisch's discovery and Griffin's concurrent work on echolocation in bats, this knowledge convinced him that problems of animal behavior were likely to be much more complex than he had imagined, due to the ability of animals to process complex information acquired from their surroundings. The sun arc theory challenged Griffin to think about the problem of migration in a new light, and fortified his skepticism of simplistic and mechanistic frameworks in the interpretation of their behavior. As he later explained, Matthews's and Kramer's work on birds "had a sobering effect on [his] reductionistic thinking."[79] Although these developments did not immediately push him toward cognitive interpretations of animal behavior, they began to legitimize ideas that would lead him down that path in the 1970s.

The first of these developments was led by British ornithologist G.V.T. Matthews's work on homing in pigeons, conducted between 1948 and 1953.[80] In a series of experiments, Matthews demonstrated that pigeons were in fact able to choose particular directions when released into unfamiliar territory, although that skill varied considerably among individuals. In general, however, the ability depended on the visibility of the sun, which pigeons evidently used for orientation. Although Griffin and

[78] Canadian ornithologist William Rowan's work was also important. See, for example: William Rowan, "Experiments in Bird Migration," *Transactions of the Royal Society of Canada*, Vol. 40 (1946): 123-135; William Rowan, "Homing, Migration, and Instinct," *Science*, Vol. 102, No. 2643 (Aug. 1945): 210-211.
[79] Donald Griffin, "Recollections of an Experimental Naturalist," p. 135-136.
[80] G.V.T. Matthews, "The Experimental Investigation of Navigation in Homing Pigeons," *The Journal of Experimental Biology*, Vol. 28 (Dec. 1951): 508-536.

others had previously suspected that birds might use the sun for orientation, Matthews was the first to demonstrate it with convincing experimental evidence.

A skilled ornithologist, Matthews raised a group of pigeons and carefully trained them in homing exercises from a young age. After hundreds of training exercises in the territory around their lofts, he took them to a mostly cleared area in unfamiliar territory and released them individually, taking care to face different directions as he let each bird loose. He observed each as it flew away, and recorded the direction in which it was flying at the 'vanishing point' (the point at which he lost sight of the birds in his binoculars, approximate 1-2 miles away). He discovered that pigeons that flew within 30 degrees of the home direction returned to their lofts at higher speeds and more frequently than others, thus demonstrating a positive correlation between homing performance and a generally correct initial flight direction.[81] The next step was to determine how certain pigeons chose the correct direction.

In these experiments, Matthews employed a group of pigeons that were rigorously trained to fly in a specific direction upon being released. This was a long-established technique, accomplished by consistently releasing pigeons in the same cardinal direction in relation to their lofts.[82] Matthews then took the pigeons into unfamiliar territory in the opposite direction of their lofts ("off the training line"). In the initial trials, most pigeons flew in their training direction, and many never found their way home. However, in further experiments with birds that had more extensive training, he found that a majority flew not in the training direction, but within 30 to 40 degrees of their home direction

[81] G.V.T. Matthews, "The Experimental Investigation of Navigation in Homing Pigeons," p. 510.
[82] This directional training in fact dates back several hundreds of years, as it was used to train carrier pigeons.

(nearly opposite their training direction).[83] Furthermore, Matthews showed that these pigeons were able to maintain the correct heading over long stretches of unfamiliar territory.[84] This was a remarkable homing ability, which suggested that pigeons were capable of choosing the correct direction regardless of their training.

Matthews was initially uncertain as to how the pigeons accomplished such feats. He ruled out random searching, since his experiments showed that pigeons mostly maintained the same heading as they flew across unfamiliar territory. He also rejected Yeagley's magnetic theory, as did most ornithologists.[85] One important clue, however, was that his pigeons did not home as well in overcast skies. To account for these data Matthews theorized a possible solution, which held that pigeons could measure the arc of the sun's motion across the sky. He supposed that they were capable of estimating the altitude of the sun and the time that it would reach its highest point, and that they could compare those measurements with that of their home loft. If the pigeons could then "interpret the difference between the two sets of measurements," they should be able to home in the correct direction, as they had in his experiments.[86] The theory, then, relied on the assumption that birds possessed a biological clock of some sort, as they were capable of keeping track of the time that it took the sun to move across the sky. However, as Matthews mused, "there is little evidence of any independent time-keeping mechanism in birds, and none as to its accuracy, but some form of physiological chronometer cannot be

[83] G.V.T. Matthews, "The Experimental Investigation of Navigation in Homing Pigeons," p. 518-519.
[84] G.V.T. Matthews, "The Experimental Investigation of Navigation in Homing Pigeons," p. 525.
[85] Griffin had previously exchanged letters with Matthews in 1948, which were sparked in part by the Yeagley controversy. Matthews was wholly unimpressed by Yeagley's work, complaining to Griffin, "Some antidote to Yeagley is clearly required." G.V.T. Matthews to Donald Griffin, 7 December 1948, Series 1, Box 7, Folder 79, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[86] G.V.T. Matthews, "The Experimental Investigation of Navigation in Homing Pigeons," p. 529.

ruled out of hand."[87] In fact, he was not alone in suggesting the possible existence of a physiological clock, and over the course of the 1950s many physiologists, ecologists, biochemists, and ethologists became increasingly interested in the concept.[88] For the time being, however, Matthews simply needed to assume that it existed in some form in order to make his theory work. Better yet, he needed experiments that could demonstrate that his theoretical assumptions were true.

Over the next few years, Matthews conducted extensive research seeking to demonstrate the validity of his theory. In one set of experiments, his pigeons learned to select food according to the position of an "artificial sun" in laboratory conditioning experiments. By feeding birds at different times of the day, he showed that pigeons could be conditioned to choose the location of a food stimulus according to the shifting angle of the artificial sun. Thus, he concluded, pigeons were capable of perceiving and reacting to the fixed angle to the sun.[89] While the theory relied on the existence of some kind of biological clock, Matthews was unable to specify the physiological basis of the clock. Nevertheless, more experiments in the field with pigeons seemed to indicate that partially cloudy conditions—when the sun was occasionally visible as opposed to fully overcast skies—affected homing in ways that suggested that birds did rely on the sun in order to choose the correct direction.[90] His theory was supported by further experiments on Manx shearwaters, a species famous for its impressive migrations that span thousands of miles. He found that shearwaters were remarkable at homing from unfamiliar territory, and that

---

[87] G.V.T. Matthews, "The Experimental Investigation of Navigation in Homing Pigeons," p. 530.
[88] On the biological clock, see: Arthur T. Winfree, *The Timing of Biological Clocks* (New York: Scientific American Books, 1987).
[89] G.V.T. Matthews, "The Relation of Learning and Memory to the Orientation and Homing of Pigeons," *Behaviour*, Vol. 4, No. 3 (1952): 202-221.
[90] G.V.T. Matthews, "Sun Navigation in Homing Pigeons," *The Journal of Experimental Biology*, Vol. 30, No. 2 (1953): 243-267.

their ability, like the pigeons, depended entirely on the visibility of the sun. In overcast skies, or nighttime releases from unfamiliar territory, the shearwaters were unable to return or did so substantially slower as compared to releases in clear skies.[91] Although the sun arc theory was not accepted quickly, additional evidence accumulated throughout the 1950s led to its increasing popularity until eventually most ornithologists recognized that it was one of the major keys to bird navigation.[92]

Complementing Matthews's work on bird navigation was that of German ornithologist Gustav Kramer at the Max Planck Institute for Animal Biology in Wilhelmshaven. Kramer took a laboratory-based approach to the problem of orientation, and in his experiments he employed starlings, a wild species with well-known migration routes in northern Germany. Using a large, circular orientation cage, Kramer tested the direction that starlings flew in a number of experimental conditions.[93] He found that by raising starlings and caging them during their vernal migratory period, he could induce "Zugaktivität," or migratory restlessness. When starlings entered this period of increased excitement and activity, they showed a strong and definite tendency to fly toward the northeast, the natural direction of their migration.[94] Like Matthews's pigeons and shearwaters, however, their ability to choose the correct direction depended on having a clear view of the sky above. Thus Kramer too held that the solar theory of orientation was the key to unlocking the mystery of bird migration.

---

[91] G.V.T. Matthews, "Navigation in the Manx Shearwater," *The Journal of Experimental Biology*, Vol. 30, No. 3 (1953): 370-396.
[92] Karl von Frisch's work on bee orientation and the "dance language" of the honeybee lent support to this theory, since he had shown that bees were capable of detecting the motion of the sun across the sky, as well as the direction of the polarization of light.
[93] The cage, which Kramer designed, could be rotated for these experiments.
[94] Gustav Kramer, "Experiments on Bird Orientation," *Ibis*, Vol. 94 (1952): 265-285.

To further confirm his findings, Kramer installed several inward-facing mirrors around the perimeter of the circular cage. By opening specific windows in the room surrounding the cage, and placing mirrors within it at particular angles, Kramer was able to shift the apparent position of the sun based on the starlings' perspective. These adjustments indeed had the predicted effect, causing the birds to move in the apparent direction of northeast, depending on the direction in which they sensed the sun.[95] Another ingenious variation demonstrated that starlings could determine absolute direction in conditioned feeding experiments. Kramer installed identical food compartments around the perimeter of the cage, and placed food within a compartment that was in a specific direction relative to where the starling was released into the cage. The entire cage could be rotated in order to prevent the starlings from using particular cues within the room or the cage itself in order to select the correct compartment. Within about two weeks of training, the birds demonstrated the ability to use the sun's position in order to determine absolute direction, and thereby choose the compartment containing the food. And they were able to do so within a margin of error of about 30 degrees.[96]

During the late 1950s, further research on sun compass orientation and the biological clock expanded the scientific study of bird migration, and new questions emerged concerning the ability of birds to utilize complex sources of information. For example, Kramer and Matthews found that some birds relied not only on the sun for directional orientation, but also on the positions of the stars when navigating at night. As surprising developments such as this came to the fore, the simpler, mechanistic conception of migration based on random exploration and simple environmental cues

[95] Gustav Kramer, "Experiments on Bird Orientation," p. 265-267.
[96] Gustav Kramer, "Experiments on Bird Orientation," p. 268-270.

gradually faded. For his part, Griffin turned his focus back to bats, although he remained an active contributor in the field of bird migration for the rest of his career.

The theory of sun compass orientation did not solve the whole problem of migration, but it—like von Frisch's work—suggested that biologists needed to reexamine their assumptions about the complexity of animal behavior in order to gain a full understanding of such behavioral phenomena. If birds and bees could use the position of the sun and stars to orient themselves, and to make judgments about time and its relationship to the sun's position, then the whole problem of migration would be cast in a new light. His excitement about these new advances led Griffin to write a book, *Bird Migration: The Biology and Physics of Orientation Behavior* (1964), for which he received the prestigious Phi Beta Kappa Science Book Award.[97] No longer could birds be thought of as physiological machines that merely reacted to environmental stimuli; rather, Griffin began to see them as agents that were capable of acquiring information about their environments from different sources, processing that information, and using it to guide their behaviors. This type of thinking pushed Griffin further away from simple mechanistic frameworks, and in the direction of cognitive interpretations of animal behavior. The transformation, however, did not happen overnight. And in addition to these developments, his own work on echolocation contributed to this new way of thinking.

---

[97] Donald Griffin, *Bird Migration: The Biology and Physics of Orientation Behavior* (New York: Anchor Books, 1964).

Listening in the Dark: the Versatility of Echolocation

In this final section, I analyze several developments in the study of echolocation during the 1950s and 1960s that further demonstrated the surprising complexity and versatility of animal behavior. This new knowledge about bats, like that generated by research on other winged creatures, resulted from the reciprocal analysis of behavior, ecology, and sensory physiology. The most important of these findings was that bats used echolocation to hunt insects. But Griffin also discovered that their target discrimination was impressively refined, as they were able to extract extraordinarily detailed information about different objects via echolocation. Thus by the late 1950s, he had come to understand echolocation as a "highly versatile mode of perception," which served as the main "sensory window" available to bats.[98] And the versatility of echolocation, which was found to be used in a variety of behavioral contexts and to accomplish different tasks, led him to view bats as active agents that wielded their specialized sensory tool in a highly specific and precise manner. Gradually, he gave up the idea that echolocation was in any true sense an "automatic" process. In this new conception, he ceded more agency to the bats themselves, who modified the physical properties of their signals according to the disparate purposes for which they used them.

As explained in my third chapter, Griffin was truly surprised in 1951 to discover that bats used echolocation for hunting insects.[99] Before then, he had assumed that it was primarily used for obstacle avoidance, and perhaps for other relatively simple tasks such as locating the entrance to caves.[100] That bats might employ it in a complex manner to

[98] Donald Griffin, "Recollections of an Experimental Naturalist," p. 138.
[99] See the third chapter of my dissertation, "The Wartime Discovery of Echolocation."
[100] Griffin's first publication on hunting via echolocation was in 1951: Donald Griffin, "Acoustic Location of Insect Prey by Bats," *Anatomical Record*, Vol. 111, No. 3 (1951): 448-449.

hunt insects on the wing simply seemed too incredible, although thinking about bats in the context of sonar and radar surely validated this possibility. As he explained in the initial stages of that research, "It is certainly reasonable to assume that they do, since their avoidance of small inanimate objects is so clearly based on this natural analogy to radar or sonar instruments."[101] It is also likely that von Frisch's demonstration that bees were capable of complex spatial and temporal calculations in their solar orientation and dance language led Griffin to question whether bats too could accomplish more complex feats using their own refined mode of perception. At the very least, von Frisch's discovery legitimized such inquiry into the behavioral complexity of higher animals.

Griffin's discovery was made possible by studying the behavior of bats in their natural environments, since it was exceedingly difficult to coax them into hunting in the laboratory.[102] Although this required special technical efforts to mobilize his ultrasonic equipment and experimental setup, he was eventually able to capture and analyze the acoustic record of both big brown bats (*Eptesicus fuscus*) and little brown bats (*Myotis lucifugus*). He analyzed the acoustic properties of the echolocation signals associated with hunting behavior, firmly concluding that the bats "employ the process of echolocation for more precise and complicated types of orientation than the mere avoidance of static obstacles."[103] He also stressed, however, that his conclusions were limited to the particular species that he studied, and suggested that there might be significant differences in the hunting strategies used by other groups of bats.

---

[101] Donald Griffin, "At What Distance Can a Flying Bat Perceive Small Objects," *Journal of Mammalogy*, Vol. 32, No. 4 (Nov. 1951): 487-488.
[102] Donald Griffin, "Bat Sounds under Natural Conditions with Evidence for Echolocation of Insect Prey," *Journal of Experimental Zoology*, Vol. 123, No. 3 (Aug. 1953): 435-465.
[103] Donald Griffin, "Bat Sounds under Natural Conditionss," p. 455.

In his analysis, Griffin placed a new emphasis on the role of frequency modulation in the bat's ultrasonic pulses. Signal theory in radar and sonar technology held that frequency modulation was useful in detecting small, moving objects, and thus Griffin proposed that it would be advantageous for the echolocation of insects at close range. As he explained at the time to James Brantley, a radar engineer at the Cornell Aeronautical Laboratory: "I have evidence that the frequency modulation is under the bats' control, and…I am strongly inclined to believe that this frequency modulation has a very considerable significance [in their hunting behavior]."[104] Griffin also proposed that such modulations would be useful in discriminating the finer details of the objects that bats perceived: "such variations in the amplitude and frequency pattern of the echo could theoretically convey to the bat rather detailed information about a small target."[105]

Yet another advantage of frequency modulation was that it rendered the bat's signal less susceptible to jamming by those of other bats and by ambient noise, and so Griffin began to study the biophysics of jamming avoidance in the late 1950s. He had wondered about this for several years, as the problem was an important and obvious one in radar and sonar development. With his graduate student Alan Grinnell, he conducted a series of experiments to assess obstacle avoidance in adverse noise conditions in the laboratory.[106] By filling the room with intense ultrasonic sound, they sought to discover the degree to which bats were able to filter out the external noise in order to navigate via echolocation successfully. Interestingly, these experiments were in fact directly

---

[104] Donald Griffin to James Brantley, 31 March 1954, Series 1, Box 1, Folder [Corr. Bra-Bru], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. Brantley became interested in Griffin's work on bats due to its connections to radar, and wrote him inquiring about the role played by frequency modulation and the Doppler effect.

[105] Donald Griffin, "Bat Sounds under Natural Conditions with Evidence for Echolocation of Insect Prey," p. 439.

[106] Donald Griffin and Alan Grinnell, "Ability of Bats to Discriminate Echoes from Louder Noise," *Science*, Vol. 128, No. 3316 (Jul. 1958): 145-147.

analogous to Griffin's wartime research on military communications at the Psycho-Acoustic Laboratory. He and Grinnell supplemented this behavioral research with neurophysiological analysis to determine if the bat's auditory cortex was particularly suited to the perception of pulses of sound. Using standard electrophysiological techniques, Grinnell set out to determine the "neural correlates" of echolocation by measuring the effect of sound on the production of electrical activity in the inferior colliculus, the area of the brain associated with auditory processing. He and Griffin thus measured indirectly the bat's sensitivity to pulses versus continuous tones, and found that the bat's high signal-to-noise ratio allowed them to discriminate the echoes of their ultrasonic pulses from background noise.[107] Griffin also employed obstacle avoidance experiments to measure the sensitivity of echolocation—that is, to determine what kinds of objects were detectable by echolocation, and at what distances bats could appreciably perceive them. In these experiments, which were supported by the Office of Naval Research, he and Grinnell performed extensive tests to correlate modifications of the physical characteristics of echolocation signals with changes in the size and distance of the objects being detected.[108]

Griffin thus spent a large part of the 1950s and early 1960s conducting experiments both in the wild and in the laboratory on the behavior of bats and the biophysical properties of echolocation that accompanied those behaviors. The behavioral plasticity as demonstrated by the bat's use of echolocation for various purposes

[107] Donald Griffin and Alan Grinnell, "Neural Correlates of Echolocation in Bats," *Federation Proceedings*, Vol. 17, No. 1 (1958): 61; Alan Grinnell and Donald Griffin, "The Neurophysiology of Audition in Bats," *Anatomical Record*, Vol. 134, No. 3 (Jul. 1959): 574; Alan Grinnell and Verity Grinnell, "Neural Correlates of Vertical Localization by Echo-locating Bats," *Journal of Physiology*, Vol. 181 (1965): 830-851.

[108] Alan Grinnell and Donald Griffin, "The Sensitivity of Echolocation in Bats," *Biological Bulletin*, Vol. 114, No. 1 (Feb. 1958): 10-22; Donald Griffin, Frederick A. Webster, and Charles R. Michael, "The Echolocation of Flying Insects by Bats," *Animal Behaviour*, Vol. 8, No. 3-4 (1960): 141-154.

dramatically altered his view of animal behavior. He eventually came to see their use of modulation not as an automatic mechanism, per se, but as a tunable function that bats actively manipulated while pursuing insects. These new developments led Griffin to write an expansive book on bats, *Listening in the Dark* (1958), which includes elements of natural history, systematics, sensory physiology, ethology, and philosophy of science.[109] For his efforts, the book was awarded the prestigious Daniel Giraud Elliot Prize (1958), awarded by the National Academy of Sciences every three to five years for the best book in zoology.

In *Listening in the Dark*, his magnum opus, Griffin began to state more explicitly his new view that bats were agents that actively utilized echolocation to accomplish various tasks, and he began to speculate for the first time about the subjective world of bats. He explained, "I believe we are justified in going on to infer that the whole behavior of the more specialized insectivorous bats involves primarily a world of sound rather than one of light. These bats must spend most of their lives conversing with the world around them."[110] But where he had previously described obstacle avoidance as an automatic process, he revised that view in light of new knowledge about echolocation. As he explained, "Echolocation cannot be an easy or automatic process for the bats; it must require attention, skill, and mental effort, albeit perhaps wholly unconscious effort like that involved in walking through underbrush or riding a bicycle."[111] Griffin thus argued that by studying echolocation, one could better understand the bat's own awareness of its

[109] Donald Griffin, *Listening in the Dark: The Acoustic Orientation of Bats and Man* (New Haven: Yale University Press, 1958).
[110] Donald Griffin, *Listening in the Dark*, p. 147.
[111] Donald Griffin, *Listening in the Dark*, p. 167.

surroundings.[112] In doing so he invoked new psychological concepts, such as attention, memory, and distraction, in the attempt to make sense of the bat's behavior:

> Evidently when bats are flying through familiar surroundings they rely to an increasing extent on their memory of spatial relations acquired on previous flights through the same space. Under these conditions their attention lapses, and they are easily caught napping, as it were, by newly placed obstructions. In the same way, I suspect, when they are migrating at night far above the ground they are not prepared for steel radio towers or tall buildings, and their occasional collisions with such obstacles are also the result of inattention or carelessness. Perhaps their thoughts are far away to the south, centered upon the fat beetles that they hope to catch as they swoop beneath the festoons of Spanish moss, so that they turn a deaf ear to the echoes which should warn them that the Empire State Building looms ahead.[113]

Rather than flying machines, then, bats were agents that "actively probe their environment."[114] And in fact Griffin likened their use of echolocation to "tool using," since "a bat fashions useful pulses of sound out of the air it breathes, projects them forward to explore its environment, and listens for echoes that can tell it about what lies ahead."[115] In his later work on animal consciousness, this line of thinking would take on a new significance when tool use became a common criterion for assessing the intelligence of higher animals such as apes.[116]

However, for the time being Griffin vacillated as to whether echolocation was truly a *conscious* process. For example, in a particularly telling passage he described what it might be like to be an echolocating bat:

> While all these events occur within less than one second, we can imagine processes which must be involved—even though they probably occur automatically and unconsciously—just as we describe to a novice the manipulations involved in driving an automobile. We may surmise that while

[112] Donald Griffin, *Listening in the Dark*, p. 79.
[113] Donald Griffin, *Listening in the Dark*, p. 167.
[114] Donald Griffin, *Listening in the Dark*, p. 77.
[115] Donald Griffin, *Listening in the Dark*, p. 77.
[116] For example, Jane Goodall's discovery in 1960 that chimpanzees used sticks to feed on termites became a classic illustration of tool-use as a measure of intelligence in nonhuman animals.

> resting quietly the bat emitted only a few pulses in order to keep itself posted as to where it was. On finding itself free to fly it sent out a rapid burst to be sure the way was clear, and then took off. Thirty pulses per second were enough to guide straight and level flight in the absence of immediate obstructions. But after flying a few feet our bat began to notice faint echoes from the wires and decided to increase its pulse repetition rate to about 50 per second in order to echolocate these small and difficult obstacles more precisely. Then, when it was close enough to the array of wires, the bat already had enough information about the wires, had decided upon its course betwen [sic] them, and relaxed its vigil to the extent of lowering the pulse repetition rate.[117]

Interestingly, whereas before he had insisted that echolocation "cannot be an easy or automatic process," in the passage above he refers to it as just that, although in doing so he seems to equate automatic with unconscious. In suggesting that the physiological processes associated with echolocation "probably occur automatically or unconsciously," he most likely intended to adopt a skeptical position on the question of animal consciousness, which in 1958 was still very much a scientific taboo. In fact throughout the book he frequently adopted a conservative tone about issues that were not firmly settled, and such rhetoric over the course of his career had earned him the reputation of being a hard-nosed skeptic. On the whole, however, by the late-1950s his thinking was shifting in the direction of echolocation being an intentional process rather than an automatic one. It would be several years, however, until he began to speculate openly about these ideas and develop them further.

Conclusion

Research on birds, bats, and bees forever transformed Griffin's understanding of animal behavior. He came to reject not only simple stimulus-response frameworks for interpreting behavior, but more fundamentally the philosophy of science that affirmed the

[117] Donald Griffin, *Listening in the Dark*, p. 78.

use of such “simplicity filters” in the first place. As he later explained privately to a colleague with whom he had an interpretive disagreement over bird orientation: “Concerning what I have come to call ‘simplicity filters’, you and I may be moving apart in a philosophical sense. I find myself less and less of a hard-boiled skeptic, having lived through several cases where the ‘from Missouri’ approach was proved by subsequent data to have been unduly restricted.”[118] Later in 1973, Griffin speculated about the underlying causes for what he was beginning to see as unjustified reductionism in behavioral explanations:

> I sometimes wonder whether the appeal of reductionist models does not stem in part from insecurity vis-à-vis our colleagues who can be so scornful of anyone who studies phenomena less precisely measurable than chemical reactions. But in my view the insecurity should be the other way around. Having been fortunate enough to be involved in some discoveries that in the beginning seemed to be merely romantic speculation, I am perhaps in an unusually good position to appreciate these considerations.[119]

Discoveries such as the dance language of the honeybee and the solar orientation of birds showed that animals were capable of vastly more complex behaviors than he had been conditioned to believe, and thus forever transformed Griffin’s approach to animal behavior. In his later work on animal consciousness, these various criticisms of reductionism would take center stage.

As his administrative duties once again began to consume much of his time and energy in the early 1960s, Griffin’s own research became increasingly sidelined. Although he collaborated in several important developments with his graduate students—

---

[118] Donald Griffin to Alvin Novick, 8 November 1971, Series 1, Box 7, Folder [Corr. - N], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC. The “from Missouri” idiom refers to the supposed legacy of skepticism among the people of Missouri, who must be shown the evidence in order to believe something. Hence Missouri’s sobriquet, the “Show Me” state. See: http://www.sos.mo.gov/archives/history/slogan.asp (Accessed 10 September 2015).

[119] Donald Griffin to Don E. Wilson, 10 January 1973, Series 1, Box 12, Folder [Corr. – Wie-Wy], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

including Alan Grinnell's work on jamming avoidance, and postdoctoral fellow Nobuo Suga's work on the neurophysiology of echolocation—Griffin became swamped in administrative work and other professional activities. His participation on conference committees and as a frequent referee for journals, for example, kept him out of the field for much of this time. These unwelcome sources of work and occasional frustration increased exponentially when in 1962 he reluctantly agreed to become chair of zoology within the biology department.[120]

On the whole, Griffin's research ground down to a slow output in the 1960s, and so when he was approached by Detlev Bronk and others from the Rockefeller Institute in 1965 ("Rockefeller University" as of 1968), he once again decided to head for greener pastures, this time in New York. As the head of a new interdisciplinary institute focused on animal behavior, the position guaranteed generous financial support for research, purposefully light teaching duties, and a large administrative support network. Along with Peter Marler, a British ornithologist who studied birdsong and avian communication, Griffin thus entered the latter stage of his career at Rockefeller's new venture, the Institute for Research in Animal Behavior.

As an established authority on animal behavior with a large budget, in this new setting Griffin began in the early 1970s to explore questions about animal consciousness. As part of those efforts, he became an outspoken critic of behaviorism, particularly in his defense of von Frisch's theory of the honeybee language. In a 1974 letter to von Frisch, he reflected on why the dance language theory had generated such a controversy:

[120] I am unsure why he agreed to the position. He openly disparaged administrative duties and academic politics, and so his decision to become chair of zoology is perplexing. Perhaps he was forced by implicit agreement to do so, although I have no evidence for this.

> There seems to be an almost ideological reluctance, bound up I suspect with the strong current of behavioristic reductionism that has been so prominent among behavioral scientists in America. But I am convinced that this tide has turned, and I can assure you that despite the many foolish publications from Wenner and his colleagues, almost no one takes them very seriously – at least no one whose opinion deserves respect.[121]

Griffin continued to explain that he was in the midst of working out some new ideas on the "mental continuity between animals and men," and requested that von Frisch put a critical eye to the essay once it was finished.[122] For the remainder of his career, especially in his work on animal consciousness, Griffin insisted that opposition to von Frisch's work and similar examples of animal complexity was rooted deeply in the pervasive climate of behaviorism and mechanism among students of animal behavior, especially in the United States. This and other developments led him to develop a new field, cognitive ethology, which he envisioned as the study of animal cognition and consciousness. In my next chapter, I explore Griffin's cognitive turn and the development of this field in greater detail.

---

[121] Donald Griffin to Karl von Frisch, 25 September 1974, Series 1, Box 11, Folder 105, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.
[122] Donald Griffin to Karl von Frisch, 25 September 1974, Series 1, Box 11, Folder 105, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

CHAPTER 6
Cognitive Dissidence and the Return of the Animal Mind

The Question of Animal Awareness

In 1976 Donald Griffin published a remarkable book in which he raised the specter of animal consciousness, a taboo in the mainstream of behavioral science.[1] *The Question of Animal Awareness* signaled a sharp pivot from his earlier work on the sensory physiology of animal behavior toward this new, speculative area of biology. Animal consciousness, for which he offered a "pragmatic, working definition," consisted in "the presence of mental images, and their use by an animal to regulate its behavior."[2] For most of the twentieth century, particularly in the United States, inquiry into the subjective lives of animals had been rejected as unscientific by the main currents of behavioral biology, psychology, and ethology.[3] Animal research was instead largely characterized by behavioristic and mechanistic approaches, which were championed as the royal road to the objective understanding of behavior. Although Griffin's work on the physiological basis of animal navigation shared little with behavioristic psychology, he too had ignored questions about consciousness. In his latest book, however, he argued that it was time to break free of those "obsolete strait jackets," and to return once again to

---

[1] Donald Griffin, *The Question of Animal Awareness: Evolutionary Continuity of Mental Experience* (New York: Rockefeller University Press, 1976).

[2] Donald Griffin, *The Question of Animal Awareness*, p. 5. Griffin's definition of awareness—"the whole set of interrelated mental images of the flow of events"—was similar and related to consciousness, and he occasionally used the terms interchangeably. Psychologist Gorgon Burghardt argues that during the 1970s, the term 'awareness' was widely understood as synonymous with consciousness in psychology: Gordon Burghardt, "Animal Awareness: Current Perceptions and Historical Perspective," *American Psychologist*, Vol. 40, No. 8 (Aug. 1985): 909.

[3] Ethologists were less likely than behaviorist psychologists to deny the very existence of animal consciousness, but they shared with behaviorists the belief that it was impossible to study objectively. The degree to which it was omitted from the ethological analysis of behavior varied among individual scientists, as psychologist Gordon Burghardt has observed. Konrad Lorenz, for example, merely put consciousness "on the back-burner, whereas Tinbergen ordered it out of the kitchen." Gordon Burghardt, "Animal Awareness: Current Perceptions and Historical Perspective," *American Psychologist*, Vol. 40, No. 8 (Aug. 1985): 909.

questions that had occupied biologists and psychologists at the turn of the century.[4] Drawing on the Darwinian framework of evolutionary continuity, Griffin charged that animals had mental experiences akin to those of human beings, and that it was high time to take such concepts seriously and to develop rigorous methods for their study in a new field of biology, which he termed "cognitive ethology."[5]

Griffin's act of cognitive dissidence was surprising for at least three reasons. First, animal consciousness was particularly taboo in biology. Such mentalistic concepts were exceedingly difficult to define, and more problematically, they were considered impossible to study objectively; to inquire about animal consciousness (especially in print) risked one's reputation as a serious and credible scientist.[6] Furthermore, *The Question of Animal Awareness* was his first publication of any kind on the subject. Although he had discussed it in seminars at the Rockefeller University beginning in 1974, most scientists working on animal behavior knew Griffin for his work on echolocation, and were unaware that his interests had shifted so significantly. He first spoke publicly about these subversive ideas in an address to the 1975 International Ethological Congress in Parma, Italy, but even this was an invitation-only meeting, with annual attendance restricted to about 300 scientists. As a result most of the scientific world first learned about Griffin's latest venture upon his book's publication in the summer of 1976. His

---

[4] Donald Griffin, *The Question of Animal Awareness*, p. 74.
[5] The term 'cognitive' can be a bit misleading, since Griffin intended for it to imply conscious awareness. In cognitive psychology and linguistics, however, the term signified approaches centered on information processing, and did not imply consciousness (although it could). In his later work Griffin parsed the differences in meaning more explicitly. Unless specified otherwise, I use the term throughout this chapter in Griffin's looser meaning, more-or-less equating it with scientific approaches to understanding consciousness, or subjective awareness.
[6] According to his former student James Gould, some of Griffin's colleagues and former students initially suspected that early-onset senility was to blame for his sudden shift to the cognitive. James Gould, "Thinking about Thinking: How Donald R. Griffin Remade Animal Behavior," *Animal Cognition*, Vol. 7 (2004): 1.

turn was all the more surprising given his reputation as a rigorous skeptic, working on the 'hard end' of biology.[7] Broaching the subject thus shocked many of his colleagues; perhaps paradoxically, however, it also had the effect that his claims were taken seriously. As sociobiologist Edward O. Wilson explained at the time, "the very suggestion of a cognitive ethology might have been considered dangerous or even foolish by anyone other than an experimental biologist of Professor Griffin's stature. We will owe him a debt for breaking the taboo."[8]

While his work on animal consciousness seemed qualitatively distinct from Griffin's prior scientific interests, firm continuities nevertheless linked these disparate phases of his career. In calling for its study he drew on evidence from areas of animal behavior with which he was closely familiar. He had discovered, for example, that bats occasionally ignored the information generated by their echolocation signals and instead relied on a seemingly internal mechanism for navigation.[9] The behavior of these 'Andrea Doria bats' led him to wonder about the existence of mental images, or "cognitive maps," and their potential use in the spatial orientation of bats and birds.[10] Griffin named them after the SS *Andrea Doria* because they frequently crashed despite the fact that their echolocation signals should have alerted them to the presence of obstacles. A more

---

[7] On Griffin's reputation as a skeptic, see: Charles Gross, "Donald R. Griffin," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 86 (2005), p. 14. British ethologist Marian Stamp Dawkins used the phrase "hard end" of biology when describing her surprise at Griffin's turn. Marian Stamp Dawkins, e-mail message to Richard Nash, 12 November 2015.

[8] Donald Griffin, *The Question of Animal Awareness* (New York: Rockefeller University Press, 1976). This quote appears on the dust jacket. In the previous year Wilson had published his provocative book, *Sociobiology: The New Synthesis*, which sparked a series of scientific and sociopolitical debates in the 1970s-1980s. E.O. Wilson, *Sociobiology: The New Synthesis* (Cambridge: Belknap, Harvard University Press, 1975).

[9] The SS *Andrea Doria* famously collided with the MS *Stockholm* despite the fact that both ships' sonar systems were found to be in proper working order.

[10] While working on behavioral conditioning in rats, American psychologist Edward C. Tolman first proposed the existence of cognitive maps in the 1940s. E.C. Tolman, "Cognitive Maps in Rats and Men," *The Psychological Review*, Vol. 55, No. 4 (Jul. 1948): 189-208.

intriguing line of inquiry came from the study of animal language, which took on a new significance in the 1960s with the emergence of cognitive linguistics and its implications for human thinking, information processing, and other mental processes.[11] While various forms of expression and communication had long been acknowledged in animals, symbolic language—that which utilized words and symbols with abstract meanings—was thought to be uniquely human.[12] Honeybees, however, possessed a symbolic language in the form of their gestural dancing, and further research on the versatility of their dance language led Griffin to wonder whether bees were subjectively aware while communicating with one another.[13]

Even more impressive was the recent case of Washoe, a female chimpanzee who was taught to speak American Sign Language in the late 1960s. In their groundbreaking study, American psychologists Beatrice T. Gardner and R. Allen Gardner taught Washoe dozens of gestural signs, which she spontaneously used in creative combinations to communicate with her human researchers.[14] Although Griffin never worked directly on primate communication, he was fascinated by Project Washoe and subsequent studies on simian language, writing to the Gardners that their work constituted "a major advance" in the study of animal behavior and communication.[15] Despite pronouncements from

---

[11] In the 1960s many psychologists, philosophers, and linguists began arguing that thinking was inextricably linked to human speech. Chomsky, however, charged that only humans possessed true language, and he rejected the notion that mental continuities existed between man and animals.
[12] On debates about animal language versus communication, see: Gregory Radick, *The Simian Tongue: The Long Debate about Animal Language* (Chicago: University of Chicago Press, 2007), especially p. 280-319.
[13] On the honeybee language controversy, see: Tania Munz, "The Bee Battles: Karl von Frisch, Adrian Wenner and the Honey Bee Dance Language Controversy," *Journal of the History of Biology*, Vol. 38 (2005): 535-570.
[14] R. Allen Gardner and Beatrice T. Gardner, "Teaching Sign Language to a Chimpanzee," *Science*, Vol. 165, No. 3894 (Aug. 1969): 664-672. On the Gardners' work, see: Gregory Radick, *The Simian Tongue: The Long Debate about Animal Language* (Chicago: University of Chicago Press, 2007), p. 316-330.
[15] Donald Griffin to R.A. Gardner and B.T. Gardner, 24 January 1968, Rockefeller University Archive, RG 450G875, Series 1, Box 3, Folder [Corr – G]. He also requested from them future reports on Washoe's progress.

cognitive linguists such as Noam Chomsky, who claimed that human language was essentially different from the rest of the animal kingdom, Griffin emphasized how little was actually known about animal communication, and insisted that linguistic studies of animals such as bees and chimpanzees would likely yield new insights about their mental processes. If cognitive linguistics made human thinking accessible, he reasoned, might the study of animal language provide a similar window onto the animal mind?

In addition to these empirical connections, Griffin's earlier work on animal behavior formed philosophical bridges to his work on consciousness and to his criticism of behaviorism. His firsthand experience in several unforeseen discoveries about animal perception and communication, for example, had led him to impugn the use of "simplicity filters" in restricting scientific hypotheses to their lowest order of complexity. Research on the celestial method of bird migration, for example, had shown that simple frameworks (such as stimulus-response mechanisms) were incapable of providing conclusive scientific solutions to complex behavioral problems. Thus in the 1950s Griffin had been forced to give up his exploratory theory of migration, which he had adopted due to its philosophical consistency with Morgan's canon, and to recognize that the basis of migration was far more complex than he had imagined. Similarly, Wenner's opposition to von Frisch's dance language theory had shown that the stubborn dedication to explanatory parsimony could lead to misinterpretations about the true causes of animal behavior. Griffin thus began to criticize the reductionist aversion to higher processes such as consciousness as a potentially harmful simplicity filter that was inhibiting progress in the study of animal behavior. However, this did not mean that one should speculate promiscuously with concepts for which there was little evidence; rather, his approach to consciousness was pragmatic, as he argued that there were indeed good reasons to suspect that animals had subjective experiences, and that it was the task of behavioral scientists to develop novel methods for their exploration. And rather cleverly, he turned the argument for scientific parsimony against those who denied consciousness. As he explained, the fact of evolutionary continuity between man and animals—as demonstrated by genetic, anatomical, and neurophysiological similarities—was obvious to all biologists. Consequently, the truly conservative intellectual position was to assume that mental continuities existed as well. At most, he explained, one ought to remain agnostic on animal consciousness, while nevertheless admitting that it was a legitimate scientific question.

With his book and subsequent research agenda, Griffin thus launched a new field, cognitive ethology, which was centered on the comparative and evolutionary analysis of animal thinking and consciousness. He argued that several dimensions of animal behavior—especially communication, behavioral flexibility, perception, and navigation—indicated that questions regarding the role of consciousness in behavior ought to be raised, despite the prevailing uncertainty about how to answer them. Recognizing that such a scientific venture would require developing novel concepts, evidentiary bases, questions, and methods, Griffin exhibited in this phase of his career an uncharacteristic willingness to consider tentative hypotheses as trailblazing forays into unknown territory. He also avoided wandering into treacherous byways such as animal welfare, which had become a highly controversial topic with the publication of philosopher Peter Singer's *Animal Liberation* in the previous year.[16] Although Griffin's

[16] Peter Singer, *Animal Liberation: A New Ethics for Our Treatment of Animals* (New York: Random House, 1975). Griffin never referred to Singer's work in print; when he did discuss animal welfare, it was

scientific work had obvious implications for bioethics and animal welfare, for the most part he strategically avoided those areas so as not to risk making his ideas even more unpalatable to scientists who relied on animal subjects in their research.[17]

Reflecting on his career in 1996, Griffin characterized his turn to consciousness as symptomatic of "philosopause," a period of philosophizing that scientists often experience late in their careers when their scientifically fertile days are behind them.[18] But his change was by no means the inevitable result of an otherwise skeptical scientist simply growing older, or perhaps more cynically, becoming senile.[19] Rather, particular circumstances facilitated his outspoken commitment to exploring new ideas about animal consciousness and to criticizing behaviorism. As we have seen in the previous chapter, surprising discoveries about the behavior of birds, bats, and bees played a large part in priming him to seek more complex explanations for animal behavior, and this later led him to impugn the mechanistic and behavioristic modes of twentieth-century biology and psychology. In addition, an important professional move in his later career bolstered Griffin's intellectual fortitude. In 1965 Rockefeller Institute president Detlev Bronk (1897-1975) recruited him to the behavioral science program as the director of the newly

---

typically in reference to the work of ethologists such as Marian Stamp Dawkins, who worked on the emotional continuity of man and animals.

[17] His choice not to rock the boat too greatly is analogous to Darwin's omission of human evolution in the *Origin of Species*.

[18] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography* [Vol. 2]. Ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 88. "Philosopause," obviously a metaphorical play on menopause, was one among many creative terms that Griffin coined later in his career. The analog for historians might be called 'tenurapause.'

[19] Apparently some colleagues and former students initially suspected that senility might have been to blame for Griffin's sudden turn. As the clarity and volume of his published works on animal conscious attest to, this was certainly not the case. See: Charles Gross, "Donald R. Griffin," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 86 (2005): 1-20, p. 14; James Gould, "Thinking about Thinking: How Donald R. Griffin Remade Animal Behavior," *Animal Cognition*, Vol. 7 (2004): 1.

established Institute for Animal Behavior Research.[20] Bronk, who was firmly committed to the interdisciplinary ideal, challenged behavioral scientists to ask difficult questions and to develop novel approaches to solving them by breaking down traditional disciplinary boundaries. As an established scientist with an unassailable reputation as a rigorous experimentalist, Griffin thus entered an intellectual environment that encouraged heterodox thinking about behavior.

It was in this context that Princeton philosopher Thomas Nagel accepted a visiting professorship at Rockefeller in 1973-1974. At the time, Nagel was drafting his now famous essay, "What Is It Like to Be a Bat?" in which he argued that the subjective character of experience was inaccessible to minds other than our own.[21] While he had already chosen the bat as his central subject, he met Griffin at Rockefeller and the two had "many fascinating and fruitful discussions" thereafter.[22] Perhaps more than any other factor, these conversations with Nagel prompted Griffin to speak publicly on the subject of animal consciousness.[23] In the remainder of this chapter I analyze the intellectual, professional, and disciplinary contours of Griffin's cognitive turn, a watershed in the twentieth-century study of animal behavior.

Rockefeller University and the Institute for Animal Behavior Research

In 1953 the newly appointed president of the Rockefeller Institute, Detlev Bronk, began a vigorous campaign to expand the institutional and intellectual reach of the

---

[20] The Institute for Animal Behavior Research was jointly sponsored by the New York Zoological Society, and Griffin directed it until 1969 when ethologist Peter Marler (1928-2014) took over.
[21] Thomas Nagel, "What is It Like to be a Bat?" *The Philosophical Review*, Vol. 83, No. 4 (Oct. 1974): 435-450.
[22] Thomas Nagel, e-mail message to Richard Nash, 13 August 2015.
[23] Griffin mentions his indebtedness to Nagel in the preface to *The Question of Animal Awareness*.

Institute by awarding PhDs and by adding several new interdisciplinary research programs.[24] A distinguished biophysicist and mandarin of American science, Bronk had a knack for accumulating accolades and powerful positions during his rise to the top, and he used that reputation (along with Rockefeller's substantial purse strings) to lure prestigious scientists to the Institute in the postwar era.[25] He was committed to a vision of "unified science," which he sought to establish by breaking down traditional disciplinary barriers and by bringing together innovative thinkers from disparate fields. To this end, he sought creative researchers who were willing to defy convention in the pursuit of scientific knowledge. One of Bronk's university ideals in his earlier tenure as president of Johns Hopkins, for example, was to attract scholars who would "investigate, debate and question conventional concepts and to seek new knowledge which fosters insecurity of established ways of thought and life."[26] He further applied this intellectual and institutional vision to transforming the Rockefeller Institute, where he presided from 1953 to 1968.

Immediately upon assuming the Rockefeller presidency, Bronk began expanding its interdisciplinary programs, which were heavily geared toward research and required

---

[24] The Rockefeller Institute, which in 1967-68 was renamed the Rockefeller University, is still located on the upper-east side of Manhattan. For an internal history of Rockefeller University, see: John Kobler, *The Rockefeller University Story* (New York: Rockefeller University Press, 1970); on biomedicine at Rockefeller University, see: J. Rogers Hollingsworth, "Institutionalizing Excellence in Biomedical Research: The Case of The Rockefeller University," in *Creating a Tradition of Biomedical Research*, ed. Darwin H. Stapleton (New York: The Rockefeller University Press, 2004); on interdisciplinary neuroscience at Rockefeller University, see: Darwin Stapleton, "Aspects of Instrumentation in the Neurosciences at Rockefeller University: Nobelists Herbert Gasser and H. Keffer Hartline" (paper presented at the Annual Meeting of the International Society for the History of the Neurosciences, Los Angeles, California, June 20, 2007).

[25] On Bronk's distinguished career in American science, see: Frank Brink, "[Biographical Memoir of] Detlev Wulf Bronk," *Biographical Memoirs of the National Academy of Sciences of the United States* (1978): 1-87.

[26] Johns Hopkins University, "Annual Report of the President, 1953," in *Johns Hopkins University Circulars* (1952-53), p. 16. Bronk was president of Johns Hopkins from 1949 to 1953.

minimal teaching.[27] By 1965 he had substantially increased the breadth of the Institute, and he took steps to change its name to the Rockefeller University in order to reflect that expansion and reorganization. In the 1967-1968 university catalogue, he described his vision thusly: "The University is not an aggregate of departments dealing with specialized fields of science. It is a community of scientific scholars who are free to follow their interests in any field of scholarship."[28] To strengthen the behavioral sciences, in 1965 Bronk recruited Griffin and British ethologist Peter Marler (1928-2014), an expert on birdsong.[29] He also enlisted American physiological psychologist Carl Pfaffmann (1913-1994) as a university vice-president and director of the newly formed behavioral sciences graduate program.[30] An authority on the neurophysiology of taste and olfaction, Pfaffmann was interested more broadly in the relationship between chemical sensation and behavior.[31] To add further depth and prestige to the group, in 1967 Bronk lured cognitive psychologist George A. Miller (1920-2012) away from Harvard.[32] Griffin already knew Miller, a pioneer in psycholinguistics, from their communications work at

---

[27] On Bronk's vision for Rockefeller's expansion, see: J. Rogers Hollingsworth, "Institutionalizing Excellence in Biomedical Research: The Case of the Rockefeller University," in *Creating a Tradition of Biomedical Research: Contributions to the History of the Rockefeller University*, ed. Darwin H. Stapleton (New York: The Rockefeller University Press, 2004), especially p. 26-30.

[28] Quoted in Frank Brink, "[Biographical Memoir of] Detlev Wulf Bronk," p. 67.

[29] On Marler's life and career, see: Peter Marler, "Hark Ye to the Birds," in *Studying Animal Behavior: Autobiographies of the Founders*, ed. Donald Dewsbury, p. 314-345 (Chicago: University of Chicago Press, 1985).

[30] In August 1965, Bronk finalized the arrangements aboard his yacht in Maine, where Griffin and Pfaffmann helped him convince Marler to join them. Griffin's memorabilia from the trip includes an intriguing photograph of a pensive Peter Marler, labeled "moment of decision." [Photograph of Marler, Pfaffmann], Series 1, Box 6, Folder [Corr – Ma-me], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

[31] Lorrin A. Riggs, "Carl Pfaffmann (1913-1994): A Biographical Memoir," *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 71 (1997): 261-279.

[32] On Miller's contributions to cognitive psychology and linguistics, see: Paul Edwards, *The Closed World: Computers and the Politics of Discourse in Cold World America* (Cambridge: Massachusetts Institute of Technology Press, 1997), especially chapter seven; Hunter Crowther-Heyck, "George A. Miller, Language, and the Computer Metaphor of Mind," *History of Psychology*, Vol. 2, No 1 (1999): 37-64; Jamie Cohen-Cole, "The Politics of Psycholinguistics," *Journal of the History of the Behavioral Sciences*, Vol. 51, No. 1 (Winter 2015): 54-77.

Harvard's Psycho-Acoustic Laboratory during the war.[33] The resulting behavioral sciences program, which was enhanced with additional faculty and a collaborative arrangement with the new program in philosophy, consisted of an impressive array of researchers working on behavioral problems from many disparate approaches.[34]

Griffin and Marler were tasked with developing the ethological arm of the behavioral sciences program, and to that end Griffin was appointed as the first director of the newly established Institute for Animal Behavior Research (known informally and hereafter as the animal behavior lab).[35] Initially developed and co-sponsored by the New York Zoological Society, the lab included facilities at the Bronx Zoo, the New York Aquarium, and a partnership with the William Beebe Tropical Research Station in Simla, Trinidad.[36] In 1971 Griffin helped secure an additional field station in nearby Millbrook, New York, a 1200-acre site for research on animals in naturalistic conditions. Under the lab's auspices during the late 1960s and 1970s, he continued research on bat behavior, the neurophysiology of echolocation, and the physiological basis of bird migration. He appreciated that his new position allowed him to focus on research at the expense of teaching, confessing privately to his friend Karl von Frisch, "perhaps selfishly I was ready for this sort of change."[37] In this innovative work he developed new methods to investigate animal navigation, including a radar system to track homing birds hidden in

[33] On Griffin's work at the Psycho-Acoustic Laboratory, see chapter three of this dissertation.
[34] Bronk sought to secure among its ranks philosophers interested in language, psychology, and philosophy of science. These included Joel Feinberg (philosophy of psychology), Donald Davidson (linguistic philosopher), and Harry Frankfurt (philosophy of mind). The philosophy program was established in 1967, but due to financial belt-tightening, it was scuttled in 1976, when Rockefeller administrators and trustees decided to focus solely on the natural sciences.
[35] Referred to hereafter as the animal behavior lab. Marler took over as its director in 1969.
[36] In 1969 Rockefeller took full control of the lab from the New York Zoological Society, which had other aims in mind. Also, the Simla station was scuttled in 1971 due to interpersonal problems, financial mishandling, and sociopolitical unrest in Trinidad.
[37] Donald Griffin to Karl von Frisch, 16 October 1965, Series 1, Box 11, Folder 105, RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

the clouds, along with high-altitude balloons to study the atmospheric cues (including acoustic, climatic, and olfactory) available to migrating birds.[38] He also oversaw the work of postdoctoral fellows and graduate students such as James Gould, whose honeybee research in the early 1970s confirmed von Frisch's dance language theory in the face of objections raised by Wenner and his colleagues.[39] For his part, Marler brought his birdsong expertise to bear on the general study of animal communication and sexual selection. In addition, he began studying primate communication, collaborating with Dorothy Cheney and Robert Seyfarth on the semantics of vervet monkey calls.[40]

Thus the animal behavior lab exhibited a rather broad ethological character, and Griffin and Marler were able to attract promising researchers working on a diverse range of behavioral phenomena.[41] However, the number of graduate students and postdoctoral researchers was kept low—two or three a year—a necessary consequence of the global economic downturn in the early 1970s. Rockefeller's financial model relied heavily on federal dollars, and as Griffin explained at the time, the "golden age of scientific funding" was coming to a quick and unceremonious end.[42] Nevertheless, the lab remained a stimulating intellectual environment due to the open-ended nature of Rockefeller's interdisciplinary seminars and university-wide gatherings, where neurophysiologists,

---

[38] Donald Griffin, "Oriented Bird Migration in or between Opaque Cloud Layers," *Proceedings of the American Philosophical Society*, Vol. 117, No. 2 (Apr. 1973): 117-141; Eleonora D'Arms and Donald Griffin, "Balloonists' Reports of Sounds Audible to Migrating Birds," *The Auk*, Vol. 89, No. 2 (Apr. 1972): 269-279.
[39] See chapter five, "Birds, Bats, and Bees," of this dissertation.
[40] Robert Seyfarth, Dorothy Cheney, and Peter Marler, "Vervet Monkey Alarm Calls: Semantic Communication in a Free-Ranging Primate," *Animal Behaviour*, Vol. 28 (1980): 1070-1094.
[41] Among the better known graduate students were Jack Bradbury and James Gould. The faculty also included prominent ethologists Fernando Nottebohm, who continues to research the neurophysiology of songbirds, and Roger Payne, who discovered the songs of humpback whales. On the graduate students, faculty, and postdocs working in the lab, see: Peter Marler, "Hark Ye to the Birds," p. 331-342.
[42] Griffin frequently lamented the end of the "golden age of funding"—which referred to the heyday of federal support for basic science in the 1950s and 1960s—in personal communications with colleagues and potential students.

biophysicists, ethologists, psychologists, and philosophers shared their work and discussed ideas with colleagues.[43]

By the time Thomas Nagel came to this vibrant environment as a visiting professor of philosophy in 1973-1974, he had written a first draft of what would become one of the most famous essays on consciousness in modern philosophy.[44] In "What Is it Like to Be a Bat?" he took for granted the mental continuity between man and animals, assuming that bats, like other nonhuman animals, had conscious awareness and subjective experiences. He chose bats as his subject for two interrelated reasons: first, they were relatively close to humans on the evolutionary continuum, possessing the complex neurophysiological machinery of mammalian brains. But unlike most mammals, the primary mode of perception in bats was not visual, but rather auditory. Thus their reliance on echolocation for perceiving the world around them yielded a unique subjective character, virtually unimaginable to humans. In his thought experiment Nagel argued that while scientific investigation could generate an enormous amount of data about the anatomy, neurophysiology, and behavior of bats, when it came to their subjective experience—that is, what it was like *to be* a bat—there were no answers to be had. For Nagel, subjective experience was contingent on the point-of-view of the agent, and it was therefore irreducible for the purpose of objective analysis. One could not simply imagine what it was like to be a bat. At best, he could imagine what it was like *for*

[43] In her short essay about Griffin, cognitive ethologist Carolyn Ristau recalls her time as a postdoc in his lab: Carolyn Ristau, "Donald Redfield Griffin," *Proceedings of the American Philosophical Society*, Vol. 149 (Sep. 2005): 399-411, especially p. 401-403.
[44] Thomas Nagel, "What is It Like to be a Bat?" *The Philosophical Review*, Vol. 83, No. 4 (Oct. 1974): 435-450. Philosopher Dan Dennett describes Nagel's essay as the "most widely cited and influential thought experiment about consciousness." Daniel Dennett, *Consciousness Explained* (Boston: Little Brown, 1991), p. 441.

him—from the perspective of a human being—to be a bat; to know the bat's experience was impossible.

Interestingly, Nagel took for granted that bats possess conscious awareness. And in fact, his definition of consciousness applied across the phylogenetic spectrum: "an organism has conscious mental states if and only if there is something that it is like to *be* that organism—something it is like *for* the organism."[45] While this stance may have been reasonable in philosophy, it represented a radical position in behavioral biology and psychology. According to Nagel, he and Griffin had many fascinating discussions about animal behavior and consciousness, and he claims at least partial responsibility for inspiring Griffin to explore these ideas in his later career. Griffin confirmed this in the preface to *The Question of Animal Awareness*, where he credits Nagel for supplying "an immediate spur while visiting our campus when he raised the question of whether animals have mental experiences."[46] Nagel, of course, did not merely raise that question, but answered in the affirmative. And in Griffin's ensuing book, he did likewise.

The "Satanic Verses" of Animal Behavior

In his conversations with Nagel, Griffin began seriously considering the question of animal consciousness and the climate of behaviorism that dismissed such inquiry as unscientific. During the next two years he further studied and discussed these issues with colleagues at Rockefeller, and began distilling his main ideas into a short manuscript, *The Question of Animal Awareness.* This landmark book served two interdependent goals: first, Griffin argued in favor of the mental continuity between man and animals. Like

[45] Thomas Nagel, "What is it Like to Be a Bat," p. 436. Emphasis in original.
[46] Donald Griffin, *The Question of Animal Awareness*, vii.

humans, he argued, animals likely had subjective experiences, and they were able to use simple thinking and conscious awareness in regulating their behaviors. He analyzed several lines of evidence about the complexity and versatility of animal navigation and communication, which suggested that these behaviors were likely accompanied and affected by mental processes and experiences. His other major objective was to break the taboo of animal consciousness, and in so doing to criticize the behavioristic reductionism that he felt was characteristic of biology and psychology at the time. He argued that behaviorism was an outmoded perspective, and that attempts to understand behavior based solely on the external actions of organisms—interpreted through stimulus-response mechanisms or other similarly reductionist frameworks—were wholly inadequate. According to Griffin, true understanding of behavior, like that which Darwin pursued, required investigation of the minds of animals, and how their mental lives affected their behavior.[47]

Griffin acknowledged, however, that the tide of behaviorism was beginning to ebb, which was evident by the flourishing of cognitive psychology in the 1960s.[48] Nevertheless, he argued that behavioristic assumptions were so deeply instantiated that they continued to relegate certain fundamental questions, especially about animal consciousness, to the dustbin of pseudoscience or amateurism. While cognitivism was becoming increasingly acceptable in human psychology, he observed, animals had yet to

---

[47] Charles Darwin, *The Expression of the Emotions in Man and Animals* (London: John Murray, 1872). Although Darwin's approach to mental and emotional continuity was criticized for its overreliance on anecdotal evidence, Griffin nevertheless agreed that Darwin was asking the right questions when it came to the origin of consciousness in nonhuman animals: Donald Griffin, *The Question of Animal Awareness*, p. 98-99.

[48] On the gradual emergence of cognitive psychology, see: John D. Greenwood, "Understanding the 'Cognitive Revolution' in Psychology," *Journal of the History of the Behavioral Sciences*, Vol. 35, No. 1 (Winter 1999): 1-22, especially p. 9-11. Greenwood argues against the notion of a cognitive "revolution," and instead locates the source of cognitive operational definitions in research dating to the 1920s. He nevertheless admits that a dramatic expansion of these approaches occurred during the 1950s and 1960s.

regain their minds. For example, psychologists such as George A. Miller, who rejected behaviorism, had developed new cognitive approaches to the study of language and information theory in order to quantify and reify the content of human mental processes.[49] Concepts such as *thinking* could therefore be quantified and understood as *cognition*, a form of information processing that used the discrete and quantifiable variables of human language. Likewise, *memory* could be conceived of as the precise *retention* of that information. In this way, human mental processes were stripped of their subjective character while being made accessible to apparently objective approaches. Miller's use of the computer metaphor of mind helped to clarify these ideas and to ground them in the 'hard' sciences of electrical engineering and computing.[50] As historians Paul Edwards and Jamie Cohen-Cole have shown, such approaches emerged at the expense of behaviorism's dominance in the Cold War era, along with their far-reaching political implications concerning the malleability of the human mind and human nature.[51] By the late 1960s, cognitive linguistics had cracked open a window to the

---

[49] Hunter Crowther-Heyck explains Miller's rejection of behaviorism and the development of his ideas about cognition in terms of the computer model of the mind, which served as a powerful metaphor for understanding the nature of human language and thinking. According to Crowther-Heyck, the computer model grounded cognitive approaches in experimental, 'hard' science (computer science and engineering), while operationalizing terms that had previously been considered mentalistic, or purely subjective. More recently, Jamie Cohen-Cole has argued that much of Miller's and Chomsky's collaborative research on psycholinguistics actually militated against the conception of the mind as a computer-like machine. See: Hunter Crowther-Heyck, "George A. Miller, Language, and the Computer Metaphor of Mind," *History of Psychology*, Vol. 2, No. 1 (1999): 37-64; Jamie Cohen-Cole, "The Politics of Psycholinguistics," *Journal of the History of the Behavioral Sciences*, Vol. 51, No. 1 (Winter 2015): 54-77.

[50] Hunter Crowther-Heyck, "George A. Miller, Language, and the Computer Metaphor of Mind," *History of Psychology*, Vol. 2, No. 1 (1999): 37-64. See also: Paul Edwards, *The Closed World: Computers and the Politics of Discourse in Cold World America* (Cambridge: Massachusetts Institute of Technology Press, 1997), especially chapter seven.

[51] Paul Edwards, *The Closed World: Computers and the Politics of Discourse in Cold World America* (Cambridge: Massachusetts Institute of Technology Press, 1997), especially chapter seven; Jamie Cohen-Cole, *The Open Mind: Cold War Politics and the Sciences of Human Nature* (Chicago: University of Chicago Press, 2014), especially chapters six and seven. Cohen-Cole argues that interdisciplinary sciences such as cognitive psychology were used by politicians and reformers to argue in favor of the view that the human mind was indeed open, and thus that human nature was not fixed. Similarly, cognitive psychologists

human mind ever so slightly. However, few psychologists were willing to extend these applications to animals, and talk of animal consciousness was still nowhere to be found.

Animal communication played a central role in Griffin's critique of behaviorism and in his arguments supporting the reality of animal consciousness. The reasons for this are twofold. First, cognitive linguistics constituted an acceptable method for subverting behaviorism and gaining scientifically legitimate access to the human mind. By narrowing the distinction between human and animal language, Griffin hoped to illuminate an analogous pathway for exploring the animal mind. Second, and relatedly, the linguistic behaviors of animals were suggestive of complex mental processes. As he argued, if even the most skeptical scientists were to observe such behaviors in humans, then they would almost certainly conclude that those activities were accompanied by conscious awareness. By demonstrating the complexity of animal communication, therefore, Griffin hoped to show that it was actually unparsimonious to assume that animals *were not conscious* of their linguistic behaviors. Human language implied the existence of subjective experiences, and he therefore insisted that the most conservative intellectual position was to assume that animal language indicated something similar.

Thus one of his major strategies was to demonstrate that certain characteristics of animal communication satisfied criteria that were assumed to be unique to human language. These included concepts such as displacement, flexibility, productivity, and creativity, and Griffin was keen to show evidence of such linguistic complexity even in insects, despite their phylogenetic distance from man. The honeybee dance language, for example, showed that bees encoded precise temporal and spatial information in their

---

drew on the popular discourse of open-mindedness to bolster their own intellectual and disciplinary objections to behaviorism.

dances, which signaled the locations of food and other biological resources. According to Griffin, this constituted linguistic *displacement*, a term that signified the ability to communicate information about objects remote in time and space.[52] Other research had shown that bees were flexible in their dances, which they adapted when performing on a horizontal surface as opposed to the typical vertically oriented plane of the honeycomb. On horizontal planes, the waggle dances pointed directly toward the food source, as opposed to taking into account the angle of sun relative to the vertical plane. Hence, the symbols and their interpretations changed, but their significance did not. This, Griffin explained, was no simple task, as it required that both parties understand changes to the linguistic rules given the physical context of their communication.

Von Frisch's colleague and former student Martin Lindauer had also shown that depending on the context, the dances signaled the locations of different resources such as potential hive sites, nectar, pollen, or water.[53] Laboratory experiments even showed that they could indicate the location of types of objects that they had never before encountered. Lindauer also found that bees used a variation of the waggle dance to coordinate and to orient swarming behaviors, which in a very real sense constituted a new linguistic phrase. As Griffin explained, these dances signaled a "Let's go!" imperative, which was followed by massive swarms.[54] These linguistic behaviors, according to Griffin, satisfied the criterion of *productivity*, or the ability to signify new meanings using extant words or concepts.[55] The versatility of the bee language meant that they could convey information about different objects, and that other bees understood the messages

---

[52] Donald Griffin, *The Question of Animal Awareness,* p. 37.
[53] Martin Lindauer, "Schwarmbienen auf Wohnungssuche," *Zeitschrift für Vergleichende Physiologie*, Vol. 37 (1955): 263-324.
[54] Donald Griffin, *The Question of Animal Awareness,* p. 24.
[55] Donald Griffin, *The Question of Animal Awareness,* p. 37.

in context. Attempts to explain such behavior by stimulus-response mechanisms were wholly inadequate. Griffin also pointed to recent evidence of language acquisition in chimpanzees such as Washoe, who learned over 130 American Sign Language gestures. Not only did she learn the signs and use them appropriately to communicate with humans, but Washoe was able to combine several words creatively to form new meanings. For example, some phrases seemed to express Washoe's desire or intent to do certain activities or acquire objects.[56] According to Griffin, the use of multiple linguistic units to create new meanings demonstrated what George Miller termed "combinatorial productivity," an ability that he had previously argued was unique to man.[57] Chimpanzees and bees, it seemed, were capable of using language much as in the same way as humans.

But did these complex linguistic abilities imply consciousness? Griffin observed that if such communicative behaviors were displayed by humans, surely most behavioral scientists would attribute them to complex mental processes that were accompanied by conscious awareness. However, in animals, Griffin argued, such versatility "raises basic questions for which we had been poorly prepared by the behavioristic tradition in psychology or the comparable reductionism in biology."[58] Indeed, he argued that the use of language in chimpanzees and honeybees likely indicated the presence of thoughts. At the very least, Griffin argued, one ought to consider Washoe's desires for objects and her other creative uses of language as suggestive of underlying subjective experiences. Treating these behaviors as such, Griffin argued, would allow scientists to develop "a

---

[56] R. Allen Gardner and Beatrice T. Gardner, "Teaching Sign Language to a Chimpanzee," *Science*, Vol. 165, No. 3894 (Aug. 1969): 664-672, especially p. 670-672.
[57] George A. Miller, *The Psychology of Communication* (New York: Bantam Books, 1967), p. 72-77.
[58] Donald Griffin, *The Question of Animal Awareness,* p. 25.

unifying framework into which many complexities of animal behavior can be fitted."[59] And by analyzing their language in terms of its subjective content, he continued, "perhaps we can understand how, and to what extent, animals make sense of the flow of events of which their behavior forms a part."[60]

In addition to linguistics, Griffin drew on evidence from studies of navigation in birds and bats. As I have explored in previous chapters, he had come to understand bat echolocation as an active process, requiring both attention and skill, which was therefore susceptible to occasional breakdowns when bats for one reason or another lost focus. Moreover, he saw an elegant versatility in the bat's use of echolocation for different purposes. As he explained, "Echolocating animals adjust and adapt the properties of their sonar systems for different modes of operation under varying conditions, and in most cases we are still uncertain of the extent of these adaptive changes in sonar technique."[61] The bird's method of celestial orientation was also suggestive of complex neural mechanisms, and research on navigation had shown their ability to use several different sources of information in order to navigate in shifting environmental conditions. Like Andrea Doria bats, these birds possibly used internal cognitive maps, consisting of mental images, which were useful and necessary for navigation. At the very least their complex behaviors were indicative of highly advanced neurophysiological processes, and Griffin argued that it was no large leap to assume that conscious awareness would likely be useful to the animals utilizing such complex modes of perception.[62] Nevertheless, he

---

[59] Donald Griffin, *The Question of Animal Awareness,* p. 61.
[60] Donald Griffin, *The Question of Animal Awareness,* p. 61.
[61] Donald Griffin, "Comments on Animal Sonar Symposium," *The Journal of the Acoustical Society of America*, Vol. 54 (1972): 137-138.
[62] Ethologist William Homan Thorpe had suggested a similar line of thinking in 1974, although he did not develop his ideas as fully as Griffin did in his book. W.H. Thorpe, "Reductionism in Biology," in *Studies in*

freely admitted that “on strictly logical grounds, complexity of behavior and conscious awareness are neither commensurate with or necessarily related to one another in any way.”[63] And as Wenner’s opposition to von Frisch had shown, there was no shortage of reductionist strategies to explain away complex behavior with simplistic mechanisms. However, Griffin continued, “in the 1970s, the crippling limitations of such intellectual mypoia [sic] should be clearly apparent; the simplicity often lies not in the behavior, but in its description.”[64] He concluded by observing, once again, that if one were truly committed to the spirit of parsimony, then he ought to remain agnostic as to whether conscious awareness accompanied such complex behaviors.

Much of this evidence was merely suggestive. And given the difficult problem of consciousness, coupled with the fact that for decades it had been compartmentalized in biology, Griffin knew that he would have to offer a potential methodology for studying it objectively. Since cognitive linguistics seemed to be the most promising path toward understanding the human mind, and many of the linguistic behaviors of animals were complex and suggestive of subjective awareness, he explained that the study of animal language was the most likely candidate for opening a window to the animal mind. Other methodologies might prove more effective once scientists began to study consciousness seriously, but for the time being, language seemed best. And within that area, sign language in chimpanzees, given their behavioral and genetic proximity to man, was the best place to start.

---

the Philosophy of Biology, Reduction, and Related Problems, eds. Francisco J. Ayala and Theodosius Dobzhansky (Berkeley: University of California Press, 1974), p. 108-138.
[63] Donald Griffin, *The Question of Animal Awareness,* p. 52.
[64] Donald Griffin, *The Question of Animal Awareness,* p. 52.

Griffin's proposed method was one of "participatory investigation."[65] It harkened back to introspective psychology at the turn of the century: by conversing with subjects about their thoughts and feelings, it was thought that the psychologist could create an accurate representation of the content of their subjective states, and coordinate that information with outward behaviors. As difficult and unprecedented as it may have seemed, Griffin nevertheless thought that communicating back and forth with animals was theoretically possible, and that it was likely to yield important evidence about the inner workings of animal minds. While chimpanzees seemed promising insofar as they could communicate with researchers using sign language, other animals would surely prove more difficult. Playback experiments were a possible solution. In this research, the communicative sounds and vocalizations produced by animals in known circumstances—warning cries in vervet monkeys, for example—were precisely recorded. They were then played back in different experimental conditions in order to understand what they signified, how linguistically flexible they were, and how such communications affected animal behavior.[66] Another possibility, he imagined, would be to use animal models, such as tiny mechanical 'insects' that were able to mimic the gestural dances of honeybees. These ideas were admittedly rudimentary, Griffin admitted, but one had to start somewhere.

Throughout the book, Griffin deployed several empirical and logical arguments to develop his case for consciousness. As we have seen, one of the most effective was turning the logic of scientific parsimony against behaviorism, which championed such explanatory simplicity. For example, a behaviorist view of the human mind, such as

---

[65] Donald Griffin, *The Question of Animal Awareness,* p. 89-90.
[66] On the history of playback experiments, see: Gregory Radick, *The Simian Tongue* (Chicago: University of Chicago Press, 2007), especially p. 322-370.

Griffin's doctoral advisor Karl Lashley's, reduced all mental phenomena to the effects of neurophysiological processes.[67] But mounting evidence showed that the differences between animal and human neurophysiology were only a matter of degree, not of kind. Furthermore, the flexibility and complexity of animal behavior—particularly in linguistic behaviors—suggested the existence of sophisticated neurophysiological machinery. Griffin therefore argued that the more conservative view was to assume mental continuity between man and animals, rather than the opposite.

Griffin also argued from history, charging that the initial generations of behaviorists had forgotten the particular circumstances in which guiding frameworks such as Morgan's canon and Watson's behaviorist manifesto were developed.[68] As Griffin explained, these ideas flourished during a period in which George Romanes's uncritical anthropomorphism, along with his overreliance on anecdotal and introspective evidence, had sullied the reputation of comparative psychology. Morgan's canon, Griffin argued correctly, was originally intended to ensure that explanations of behavior were rigorous, experimentally proven, and untarnished by anthropomorphic attitudes that attributed human emotions and reasoning to the behavior of animals. Morgan never intended to deny wholesale that animal behavior could be psychically complex; rather, he simply wanted to curb the anthropomorphic enthusiasm that had threatened the legitimacy of Darwinian psychology.[69] Similarly, Watson's commitment to behaviorism

---

[67] On Lashley's approach to mind, see: Nadine Weidman, *Constructing Scientific Psychology: Karl Lashley's Mind-Brain Debates* (Cambridge: Cambridge University Press, 1999), especially p. 32-48. After about 1923, Lashley was no longer a behaviorist in the Watsonian sense. However, he maintained that subjective experiences were nothing more than the effects of neurophysiological processes, and therefore his reductionist conception of consciousness was consistent with later behaviorists such as B.F. Skinner.
[68] Donald Griffin, *The Question of Animal Awareness,* p. 71-73.
[69] Griffin's interpretation of Morgan's canon was correct, as historian Alan Costall has shown. Alan Costall, "How Morgan's Canon Backfired," *Journal of the History of the Behavioral Sciences*, Vol. 29 (Apr. 1993): 113-122.

was forged in the flames of infamous cases such as Clever Hans, the horse that could apparently solve complex mathematical problems.[70] In 1907, psychologist Oskar Pfungst subsequently showed that Hans had simply relied on extremely subtle cues in its handler's behavior, which signaled the correct answers to seemingly difficult questions. The cues were so subtle, in fact, that even the handler himself, Wilhelm von Osten, was unaware of them. This early-twentieth century episode taught behavioral scientists a sobering lesson about experimental rigor and the subtlety of perception. Moreover, the case showed that apparent complexity—especially in the behavior of animals—could actually be the product of rather simple explanations. Griffin charged that subsequent generations of behaviorists had forgotten that these historical circumstances were responsible for the ensuing devotion to behavioristic and mechanistic approaches. If later generations had properly recognized these contingencies, then perhaps they would not treat behaviorism as received wisdom, but would instead see it as a useful methodology for certain kinds of analysis. Questions regarding animal consciousness, he concluded, were not inherently unscientific, but historically contingent.

When it came to charges of anthropomorphism, Griffin attacked the logical basis of that critique. As he explained, ideas about animal consciousness and thinking were frequently criticized as anthropomorphic, insofar as they implied that animal experiences were similar to those that humans might have under similar circumstances. Morgan formulated his canon, as we have seen, precisely to criticize this faulty reasoning. But Griffin subverted the modern anthropomorphic critique by pointing out the implicit assumption contained therein, namely, that human mental experiences were the only kind

[70] On Clever Hans and its influence on Watson and early-behaviorism, see: Robert Boakes, *From Darwin to Behaviourism* (Cambridge: Cambridge University Press, 1984), p. 78-81.

that existed.[71] Animals, he argued, may have substantially different subjective experiences, particularly when it comes to the *content* of those experiences. Nevertheless, he argued, their complex patterns of behavior and neurophysiological machinery suggested that such experiences were possible. Therefore, Griffin concluded once again that it was unparsimonious to assume that human mental experiences were the only kind to exist. He thus turned the anthropomorphic criticism on its head, explaining that the critique itself was inherently anthropocentric and conceited—a view that he would later come to term "species solipsism."[72]

Another of his discursive strategies was to argue that there were unfairly high evidentiary standards in behavioral biology, particularly when it came to subjective concepts. Again arguing from history, Griffin observed that several instances of scientific progress were the result of introducing a tentative idea, initially lacking in empirical rigor, that was nevertheless useful for investigating a complex scientific problem. The 'quark' in theoretical physics, and the 'gene' in genetics and molecular biology, for example, had proven to be extremely versatile concepts that led to fundamental discoveries in these fields. If scientists had initially rejected research that was based on those concepts because of their unproven status, then perhaps these complicated phenomena would have continued to resist scientific clarification. Hypothetical concepts were commonly accepted in physics, the 'hardest' of the natural sciences. In the behavioral sciences, however, such concepts were considered nonstarters. Griffin would later refer to this double standard as demonstrative of "paralytic perfectionism," by which he meant scientific exploration that was paralyzed by accepting only those concepts and

---

[71] Donald Griffin, *The Question of Animal Awareness*, p. 68-69.
[72] Donald Griffin, "Animal Consciousness," *Neuroscience & Biobehavioral Reviews*, Vol. 9 (1985): 615-622.

ideas that were fully formed, and for which there existed perfect evidence.[73] New areas of science, such as the cognitive ethology that he was working to establish, relied on such inchoate and tentative hypotheses to construct intellectual frameworks. Therefore Griffin argued that behavioral scientists ought to shed their reflexive tendency to banish them.

A final strategy was to avoid controversial topics that were unhelpful to his cause, regardless of their importance or relevance. Thus Griffin made a strategic choice not to discuss animal emotion or welfare. But there was a deep irony in this. As psychologist Gordon Burghardt has explained, behavioral scientists in the 1970s were actually *more willing* to accept the emotional continuity of man and animals than mental continuity. Animal consciousness was, for example, far more scientifically subversive than, say, animal pain or fear. However, where emotional continuity may have been more palatable intellectually, it was in another sense more controversial because of the rising animal welfare movement in the 1970s. Philosopher Peter Singer's provocative book, *Animal Liberation*, had just appeared in 1975, and it caused a big row among ethologists and psychologists who relied on animal subjects in their research.[74] Despite the fact that many commentators linked Singer's and Griffin's books as representing parallel movements, Griffin never mentioned Singer's views on animal welfare and generally steered clear of bioethical discussions in his published works. There is no doubt that he recognized the ethical dimension of animal consciousness, but he was already fighting an uphill battle in

---

[73] In these cases, he cleverly mused, too much rigor could lead to rigor mortis.

[74] Peter Singer, *Animal Liberation: A New Ethics for Our Treatment of Animals* (New York: Random House, 1975). On Singer's book and animal welfare, see: Marc Bekoff, "Cognitive Ethology and the Treatment of Non-Human Animals: How Matters of Mind Inform Matters of Welfare," *Animal Welfare*, Vol. 3 (1994): 75-96; Colin Allen and Marc Bekoff, "Animal Minds, Cognitive Ethology, and Ethics," *The Journal of Ethics*, Vol. 11, No. 3 (Sep. 2007): 299-317.

establishing the scientific legitimacy of animal consciousness, and thus he had little incentive to engage additional adversaries.

Griffin's book received mixed reviews. Many, such as linguist Caryl Haskins, praised him for breaking the taboo: "There can be no doubt of the importance of this emphasis, especially at this time. Certainly no one is more eminently fitted to speak strongly on the matter than Donald Griffin."[75] Others were unconvinced by his arguments, and some saw it as representing an exceedingly radical scientific position. Canadian psychologist Hank Davis, for example, would later criticize the expanded edition (1981) as the "*The Satanic Verses* of animal cognition," referencing the well-known controversy surrounding Salman Rushdie's novel.[76] Psychologist William Mason wrote the most critical review, which appeared in *Science*.[77] He criticized Griffin for failing to improve upon the unsophisticated definitions of mental concepts that he provided in the introduction, and for spending too much time building up to the "lame and unsatisfying" conclusion that many of the supposed facts of animal behavior justified an agnostic position.[78]

Mason's most biting accusation was that Griffin spilled too much ink defending basic ideas that did not require defense. That awareness would be of adaptive advantage to animals, for example, was self-evident. Of course many animals experienced internal images that were helpful in navigation, Mason continued. Beyond that, Griffin had made too much of a fuss arguing in favor of the view that animals were subjectively aware—

---

[75] Caryl Haskins, "The Evolving Mind," *Semiotica*, Vol. 23, No. 3 (1978): 381-385.
[76] Hank Davis, "Anthropomorphism Reconsidered: Animal Cognition Versus Animal Thinking," (1989), quoted in Roger K. Thomas and Rosanne B. Lorden, "Numerical Competence in Animals: A Conservative View," in *The Development of Numerical Competence: Animal and Human Models*, eds. Sarah Boysen and E. John Capaldi (Hillsdale, NJ: L. Erlbaum Associates, 1993), p. 128.
[77] William Mason, "Windows on Other Minds," *Science*, Vol. 194, No. 4268 (Nov. 1976): 930-931.
[78] William Mason, "Windows on Other Minds," p. 930.

this was a fact that "could scarcely be questioned." According to Mason, Griffin had stopped with these basic and obvious observations, and failed to go one step further in asking, for example, how such internal mechanisms may have evolved. Finally, Mason criticized Griffin's proposed methodology for exploring the animal mind. The significance of communicating with chimpanzees, according to Mason, was not that it offered a means by which humans could communicate with them to learn about their subjective states. Rather, it was that such investigations showed how they acquired and used language artificially, shedding light on their *cognitive* processes. Mason continued, explaining that while such cognitive work was not as exciting as the "Dr. Doolittle" methods proposed by Griffin, they nevertheless constituted the only true method for understanding animal minds. Contra Griffin, Mason argued that there was no true "window" to the mind of another human, let alone to that of an animal. He concluded by suggesting that decades of cognitive investigations had led to the "hardest lesson of all: There is no royal road to the mind; we are forced to approach along the only paths that are open to us, through the tortuous byways of analysis, inference, hypothesis, and reconstruction."[79]

Other reviews seemed to miss the forest for the trees. Griffin's decision to include several "rough and ready" working definitions of 'mind', 'consciousness', and 'thinking,' for example, was particularly problematic. And it resulted in exactly what he had hoped to avoid—many readers focused too much on the definitions, and quibbled over the precise language that Griffin offered. As he had explained in the introduction, the prevalence of behaviorism had prevented the serious consideration and experimental investigation of these concepts. Therefore, he merely offered unsophisticated definitions

[79] William Mason, "Windows on Other Minds," p. 931.

of them as a strategic way to get the ball rolling, so to speak. Another reviewer, British psychologist Nicholas K. Humphrey, was particularly unfair, accusing Griffin of resurrecting the animal soul.[80]

In his second edition and in subsequent books, Griffin answered his critics. To Humphrey, for example, he offered a pragmatic response: "It seems most reasonable and parsimonious to postulate, tentatively and pending new evidence, that thinking and experiencing are related in comparable ways to the functioning of the central nervous systems in various species. It contributes very little to our understanding of these difficult problems to erect and then demolish straw ghosts."[81] When it came to Mason's more substantive claims, Griffin explained that he too had missed the mark. What Griffin was calling for was an exploration of the animal mind—that is, subjective experience, consciousness, and their influences on behavior. Within Mason's cognitive approach, according to Griffin, questions about consciousness were still largely forbidden, and mental processes were reconfigured according to the tenets of information processing. Within this framework, he argued, it was unnecessary to assume that any thinking—human or animal—was conscious. Convincing behavioral scientists to move beyond cognition to consciousness thus became one of Griffin's overarching goals in the following years.[82]

With the publication of his book, Griffin thus announced to the scientific world how he would spend the remainder of his career. The study of animal consciousness became the central organizing feature of his intellectual life, and he was firmly

---

[80] Nicholas Humphrey, "The Question of Animal Awareness," *Animal Behaviour*, Vol. 25, No. 2 (1977): 521-522.
[81] Donald Griffin, *The Question of Animal Awareness*, 2nd ed. (New York: Rockefeller University Press, 1981), p. 26.
[82] Donald Griffin, "From Cognition to Consciousness," *Animal Cognition*, Vol. 1, No. 1 (Jul. 1998): 3-16.

committed to making such questions scientifically legitimate once more, as they had been in the initial decades after Darwin. Griffin continued this work at Rockefeller, where he was free to pursue such ideas that pushed the boundaries of behavioral science.

Many scientists certainly shared Mason's belief that Griffin's pursuit of animal consciousness—particularly via the method of participatory investigation—would prove unfruitful. And yet despite these initial criticisms, Griffin's work had a major influence on the study of animal behavior and consciousness. By breaking the taboo, he helped to make it respectable once again for scientists to research and to discuss animal consciousness publicly. As part of these reform efforts, in the late-1970s he began to shore up the disciplinary foundations of cognitive ethology by bringing graduate students and postdoctoral fellows interested in animal cognition and consciousness to Rockefeller University. In addition, he coordinated a special issue of the journal *Behavioral and Brain Sciences*, which was focused on the topic of chimpanzee communication and consciousness.[83] In subsequent years, *Behavioral and Brain Sciences* has become a central repository for research in cognitive ethology. Griffin also organized an international conference in 1981, "Animal Mind-Human Mind," in Dahlem (Berlin), Germany. The "Dahlem model" of international scientific workshops consisted of a weeklong conference attended by 48 individuals with the goal of promoting interdisciplinary ideas about scientific problems in an international context. He conceived the 1981 workshop to "explore the nature of the animal mind and develop new approaches to its understanding."[84] He also used his tenure as president of the

[83] *Behavioral and Brain Sciences*, Vol. 1, No. 4 (1978).
[84] Donald Griffin, introduction to *Animal Mind – Human Mind*, ed. Donald Griffin (New York: Springer-Verlag, 1982), p. 1-2. It was attended by several key figures working in animal behavior and consciousness

Guggenheim Foundation from 1979 to 1983 to fund scientific projects that focused on animal consciousness and linguistics, such as Roberth Seyfarth's and Dorothy Cheney's research on the semantic communication and perception in vervet monkeys. Finally, he continued to write books that were directed at a broad, educated audience, which included behavioral scientists and his critics. In addition to *The Question of Animal Awareness*, in the 1980s and 1990s he wrote two more comprehensive books, *Animal Thinking* (1984), and *Animal Minds* (1992).[85] The sequence of titles—from animal awareness, to thinking, to minds—reflects the further development of his thought, and the boldness with which he articulated these ideas.

Since the late 1970s, the field of cognitive ethology has expanded and flourished, and new discoveries and approaches have shed further light on the animal mind. Cognitive ethologists Colin Allen and Marc Bekoff have documented this "rapidly growing interdisciplinary field of science," observing that significant advances have occurred in the understanding of social play, anti-predation behavioral strategies, and animal communication.[86] Bekoff includes himself among the critics of Griffin's initial work for its anecdotalism and philosophical naivety, but he explains nevertheless, "few contest that it was [Griffin's] 1976/1981 book that rekindled interest in the rigorous, comparative, and evolutionary study of nonhuman animal minds."[87] And despite

---

studies, including Daniel Dennett, Marian Stamp Dawkins, Martin Lindauer, Herbert Terrace, Colin Beer, Peter Marler, and Ted Bullock.

[85] Donald Griffin, *Animal Thinking* (Cambridge: Harvard University Press, 1984); Donald Griffin, *Animal Minds* (Chicago: University of Chicago Press, 1992).

[86] Marc Bekoff, "Cognitive Ethology," in *A Companion to Cognitive Science*, eds. William Bechtel and George Graham (Malden, MA: Blackwell, 1998), p. 371. See also, Colin Allen and Marc Bekoff, "Cognitive Ethology and the Intentionality of Animal Behavior," *Mind and Language*, Vol. 10, No. 4 (Dec. 1995): 313-328.

[87] Marc Bekoff, "Cognitive Ethology: The Comparative Study of Animal Minds," in *Blackwell Companion to Cognitive Science*, eds. William Bechtel and George Graham (Oxford: Blackwell Publishers, 1995); Marc Bekoff, "Cognitive Ethology," in *A Companion to Cognitive Science*, eds. William Bechtel and behavioristic criticisms of Griffin's work, Allen and Bekoff explain, "The plethora of data and the volumes of work that are available now indicate that many scientists are very much interested in animal minds and that they are following Griffin's courageous lead in attempting to study animal cognition more rigorously than has been done in the past."[88] Collected volumes such as *Cognitive Ethology: The Minds of Other Animals* (1991) attest to the wide-ranging interest and research agendas that trace their origins to his foundational work.[89]

These new areas include patterns of behavior that are suggestive of animal awareness, due to the ways in which animals adapt their behaviors according to specific contexts and problems. The study of deception has become one important focal point in this line of inquiry. [90] Cognitive ethologist Carolyn Ristau's work on intentional deception in piping plovers, for example, focuses on these shorebirds' unique strategies for avoiding predation. When intruders near the plover's nesting areas, the birds flexibly deploy several kinds of distraction behaviors to lure potential predators away with the promise of an easy meal. These including false brooding (to indicate that no eggs are present), "broken wing displays," and other peculiar motions and vocalizations that draw the attention of the predator away from the vulnerable eggs and young in nests. The

---

George Graham (Malden, MA: Blackwell, 1998), p. 371; Cognitive psychologist Sara Shettleworth also points to Griffin's work as seminal in returning questions of animal consciousness to biology: Sara Shettleworth, "Cognitive Ethology and the Evolution of Mind," in *Cognition, Evolution, and Behavior*, ed. Sara Shettleworth , p. 475-522 (New York: Oxford Press, 1998).

[88] Colin Allen and Marc Bekoff, *Species of Mind* (Cambridge: MIT Press, 1997), p. 36.

[89] Carolyn Ristau, ed., *Cognitive Ethology: The Minds of Other Animals*, ed. Carolyn A. Ristau (Hillsdale, NJ: Lawrence Erlbaum Associates, 1991). In addition to scientific conferences and publications on the topic, popular articles about the scientific study of animal minds have been steadily produced ever since.

[90] Several studies of behavioral adaptations that were significant from the perspective of cognitive ethology, such as animal communication and deception, were also important in concurrent research in sociobiology. For example, Richard Dawkins discussed the significance of deception, although he interpreted such communication signals not as the result of the animal making a conscious decision to deceive, but rather because such behavior had "an effect functionally equivalent to deception." Richard Dawkins, *The Selfish Gene*, 30th Anniversary Edition (Oxford: Oxford University Press, 2006), p. 64-65.

plovers keenly observe the predators in order to gauge the effectiveness of their distraction strategies, modifying them as necessary in order to achieve their goals. In a wide range of experiments, Ristau has demonstrated the versatility in the distraction displays, which birds flexibly adapt according to the environmental circumstances and the behavior of the intruders. Although the biomechanics of the displays are largely genetic, as opposed to learned, plovers deploy them with great specificity. Thus Ristau has designed and interpreted her experimental results in terms of subjective intentionality: "the plover wants to lead the intruder away from nest/young."[91] While she admits that the behaviors might be entirely unconscious, Ristau maintains the importance of the cognitive ethological approach in understanding such behavior, explaining, "the stance led me to design experiments that I had not otherwise thought to do, that no one else had done, and that revealed complexities in the behavior" previously unknown.[92]

Other fruitful areas included the deception behaviors of vervet monkeys, which frequently communicate false information to one another in order to gain social advantages.[93] Ethologists Dorothy Cheney and Robert Seyfarth have shown that as a result, these monkeys have developed strategies for detecting deception, including the comparison of vocal signals based on their contextual meanings. Although much of cognitive ethology, and in particular the study of animal language, is focused on primates (especially chimpanzees), other animals such as African and Asian elephants, hognose snakes, and bottlenose dolphins are frequently employed in studies of animal

---

[91] Carolyn Ristau, "Aspects of the Cognitive Ethology of an Injury-Feigning Bird, the Piping Plover," in *Cognitive Ethology: The Minds of Other Animals*, ed. Carolyn Ristau (Hillsdale, NJ: Lawrence Erlbaum Associates, 1991), p. 97.

[92] Carolyn Ristau, "Aspects of the Cognitive Ethology of an Injury-Feigning Bird, the Piping Plover," p. 102.

[93] Dorothy L. Cheney and Robert M. Seyfarth, "Truth and Deception in Animal Communication," in *Cognitive Ethology: The Minds of Other Animals*, ed. Carolyn Ristau (Hillsdale, NJ: Lawrence Erlbaum Associates, 1991), p. 97.

consciousness, self-recognition, and cognition.[94] Studies of communication and cognition in African grey parrots constitute another thriving area in cognitive ethology.[95] These birds are not only extremely adept at learning English words for different objects, but also show rudimentary understanding of concepts such as shape and color.[96] In addition, Marc Bekoff's work on animal emotions and animal play has contributed to a greater understanding of emotional subjectivity in a variety of species.[97] More recently, primatologist Sarah Brosnan's experiments on "fairness" in monkey behavior has been analyzed in terms of intentionality and calculated decision making.[98] Despite the continuing presence of strict behaviorists who insist that the animal mind will likely forever remain in a black box, scientific inquiry into animal consciousness, self-awareness, intelligence, and communication became almost commonplace by the late-twentieth century.[99] The taboo has largely been broken, and research on such questions continues to find steady sources of funding and outlets for publication.

In the waning years of his career, Griffin wrote two short autobiographical memoirs detailing the scope of his research and his life in science. To conclude the

---

[94] Psychologist David Premack's research on language and cognition in chimpanzees is perhaps the best known in this area. See, David Premack and Ann James Premack, *The Mind of an Ape* (New York: Norton, 1983).

[95] Irene Pepperberg, "A Communicative Approach to Animal Cognition: A Study of Conceptual Abilities of An African Grey Parrot," in *Cognitive Ethology: The Minds of Other Animals*, ed. Carolyn Ristau (Hillsdale, NJ: Lawrence Erlbaum Associates, 1991), p. 97. These studies frequently appear in popular articles about animals minds. For example, see the March 2008 special edition on animal minds in *National Geographic*.

[96] For further discussion, see Irene Pepperberg, "Evidence for Conceptual Quantitative Abilities in the African Grey Parrot: Labeling of Cardinal Sets," *Ethology*, Vol. 75 (1987): 37-61.

[97] See for example, Marc Bekoff, "The Public Lives of Animals," *Journal of Consciousness Studies*, vol. 13, No. 5 (2005): 115-131.

[98] Sarah Brosnan and Frans de Waal, "Monkeys Reject Equal Pay," *Nature*, Vol. 425 (Sep. 2003): 297-299.

[99] More recently, cognitive psychologist Sara J. Shettleworth has written critically about Griffin's pursuit of consciousness, describing his work as "not always sufficiently critical, but always stimulating." Sara Shettleworth, "Do Animals Know That They Know," *Trends in Cognitive Sciences*, Vol. 5, No. 9 (Sep. 2001): 404-405.

dissertation, I consider how Griffin's memoirs reflected his broader intellectual and professional goals.

Conclusion: The Return of the Animal Mind

In 1985, Griffin wrote a short autobiographical memoir for a collected volume about the history of animal behavior research.[100] The essay eloquently recapitulates his upbringing, family, education, major research agendas, professional moves, and the intellectual trajectory of his career in science. In the final paragraph, Griffin turns to the question of animal consciousness, explaining:

> I have often wondered in recent years why it took me so long to speak up on this subject. I believe the reason was my early indoctrination in the positivistic climate of science at Harvard and elsewhere in the 1930s. Many scientific developments and much shaking up of prior ideas were necessary before I was ready to think seriously about the thoughts and feelings of animals…It does seem that my firsthand involvement in several surprising discoveries is what prepared me to shift my thinking into new and I hope fruitful channels.[101]

In a later memoir, he also explained the onset of his "philosopause" as the result of dissatisfaction with reductionism, and of having lived through several surprising discoveries.[102] Elsewhere, in a 1985 research profile for Rockefeller University, he pointed to von Frisch's work as the necessary condition for his cognitive turn. He recalled being shaken "out of my reductionistic complacency. I began to wonder whether animals might not be doing a lot of things we never imagined they could do."[103] And yet

[100] Donald Griffin, "Recollections of an Experimental Naturalist," in *Leaders in the Study of Animal Behavior: Autobiographical Perspectives of the Founders*, ed. Donald Dewsbury, p. 120-142 (Lewisburg: Bucknell University Press, 1985).
[101] Donald Griffin, "Recollections of an Experimental Naturalist," p. 140.
[102] Donald Griffin, "[Autobiographical Memoir]," in *History of Neuroscience in Autobiography* [Vol. 2]. Ed. Larry Squire, p. 68-93 (San Diego: Academic Press, 1998), p. 88-90.
[103] Fulvio Bardossi and Judit N. Schwartz, "Sensible Animals," *Research Profiles*, No. 23 (Winter 1985/86): 2.

despite these explanations, it was almost thirty years after learning about von Frisch's work that Griffin decided to speak out on animal consciousness.[104]

Although he may have publicly avoided speculating about the subjective lives of animals, his private correspondence contains an important clue as to how he thought about it, even years before he decided to break the taboo. In an intriguing 1959 letter to NIH neurophysiologist Wade H. Marshall (1907-1972) concerning the treatment of animal subjects in scientific research, Griffin showed his cards:

> I am not convinced that there is any real qualitative, moral difference, between regeneration experiments on planaria or those employing curarized frogs. Our scruples are very largely anthropomorphic, whether we like to admit this or not. No physiologist could well maintain that there was any great difference in the physiological likelihood of pain or suffering being inflicted by the same procedures applied to chimpanzees and rats; yet in terms of our own thinking as well as in public relations, I am sure we shudder more for the primate than for the rodent.[105]

It is important to note that at this point in his career, Griffin's approach to animal behavior was still largely consistent with behaviorism, insofar as he omitted from his analysis questions about animal thinking, feeling, and consciousness. Nevertheless, it is likely that his views on the subjective feelings of his experimental subjects were by no means uncommon or unorthodox among scientists working with animals, despite the prevalence of behaviorism. As historian Anne Rose has shown in the case of primatologist Robert Yerkes (1876-1956), for example, behavioral scientists were often led by practical considerations to analyze the mental and emotional lives of their subjects, even if the conventions of professional science precluded them from discussing these

---

[104] His former student James Gould complained that every time he asked Griffin what had turned him to the question of animal consciousness, Griffin gave a different answer. James L. Gould, "Thinking about Thinking: How Donald R. Griffin Remade Animal Behavior," *Animal Cognition*, Vol. 7 (2004): 1-4.

[105] Donald Griffin to Wade H. Marshall, 21 October 1959, Series 1, Box 6, Folder [Corr – Ma-me], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

dimensions in print.[106] Despite their methodological commitments to objectivity, Rose argues, scientists' pragmatic experiences with animal emotions and personalities influence the science in subtle ways.[107] This was almost certainly true for Griffin, who grew up loving wild animals, and whose experimental work was largely on bats, creatures that are notoriously difficult to care for and to keep healthy in captivity. Later in that same letter, Griffin moved from pain and suffering to the question of animal consciousness:

> My feeling is that consciousness is present as a continuum roughly paralleling the refinement of nervous systems, but that there is probably no qualitative distinction to be drawn anywhere from man to coelenterate. […] I would personally reject the trading of unquestionable mammalian suffering for limited gain in knowledge that it seems to me is involved in many ablation experiments with dogs and cats. While I would not do such experiments myself, I do not feel any sufficient moral indignation to try to prevent others from doing them.[108]

Griffin wrote this letter in 1959, fifteen years before he began to speak publically about animal consciousness. His prose shows no signs of hesitation or deference on the question of animal consciousness or subjective experience, and yet these were not areas that he openly investigated. In a little over a decade, however, he would argue that such questions were essential for understanding the complexity of animal behavior.

While he used the term indoctrination to describe his scientific education at Harvard, that is probably just for rhetorical flourish. Instead, it is likely that in moving from an amateur naturalist to an experimental physiologist—with all of the intellectual and professional considerations that that entails—Griffin merely became accustomed to

[106] Anne Rose, "Animal Tales: Observations of the Emotions in American Experimental Psychology, 1890-1940," *Journal of the History of the Behavioral Sciences*, Vol. 48, No. 4 (Fall 2012): 301-317.
[107] Similarly, historian Dan Todes has shown that in the case of Pavlov's physiological research on the digestion in dogs, the particular personalities, or characters, of his dogs played an important role in how Pavlov organized his research and interpreted his students' experiments. Daniel Todes, *Pavlov: A Russian Life in Science* (Oxford: Oxford University Press, 2014).
[108] Donald Griffin to Wade H. Marshall, 21 October 1959, Series 1, Box 6, Folder [Corr – Ma-me], RG 450G875 Donald Redfield Griffin Papers, Rockefeller University Archives, RAC.

the conventions of professional science. Years later, after enjoying a successful career and cultivating a reputation as a good and proper scientist, he found himself in a position at Rockefeller where he no longer needed to worry about convention. In this phase of his career he found himself with intellectual breathing room, where he could pause to contemplate what it was like to be a bat.

The significance of Griffin's cognitive turn, therefore, was not in somehow becoming convinced that animals were conscious and that they experienced emotional states. As we can see from the letter above, he was already convinced of that fact at least by 1959. Perhaps he never had to be convinced, for surely he did not simply ignore all of his early childhood memories of running through the woods and fields of New England, chasing down skunks, and banding bats to track their migrations. Rather, the true significance of his turn was that he finally felt compelled to speak outwardly about these—his inner feelings—and to argue against what he saw was scientific convention.

BIBLIOGRAPHY

Manuscript Collections and Archival Material

Donald Redfield Griffin Papers. RG 450 G 875. Rockefeller University Archives, Rockefeller Archive Center, Sleepy Hollow, New York.

Detlev Wulf Bronk Papers. RG 303. Rockefeller University Archives, Rockefeller Archive Center, Sleepy Hollow, New York.

Department of Biophysics Records. Special Collections. MSEL Library, Johns Hopkins University.

OSRD Reports. Division of Scientific and Technical Reports [Technical Reports and Standards]. Library of Congress, Washington, DC.

Published Primary Sources

Allen, Colin, and Marc Bekoff. "Cognitive Ethology and the Intentionality of Animal Behavior." *Mind and Language*, Vol. 10, No. 4 (December 1995): 313-328.

______. *Species of Mind: The Philosophy and Biology of Cognitive Ethology.* Cambridge: MIT Press, 1997.

Allen, Glover. *Bats.* Cambridge: Harvard University Press, 1939. Reprinted by Dover, 2004.

Barbour, Thomas. "Bats." *The Atlantic*, Vol. 175, No. 6 (June 1945): 90-93.

Bekoff, Marc. "Cognitive Ethology: The Comparative Study of Animal Minds." In *Blackwell Companion to Cognitive Science*, edited by William Bechtel and George Graham, 371-379. Oxford: Blackwell Publishers, 1995.

______. "The Public Lives of Animals." *Journal of Consciousness Studies*, Vol. 13, No. 5 (2005): 115-131.

Bragg, W.L. "Personal Reminiscences." In *Fifty Years of X-Ray Diffraction*, edited by P.P. Ewald, 533-536. Utrecht: N.V.A. Oosthoek, 1962.

Brosnan, Sarah, and Frans de Waal. "Monkeys Reject Equal Pay," *Nature*, Vol. 425 (September 2003): 297-299.

Buckley, O.E. "[Radar]." *Bell Laboratories Record*, Vol. 21 (June 1943): 333.

Carson, Rachel. "The Bat Knew it First." *Collier's Weekly* (November 1944): 24.

______. *Silent Spring.* Boston: Houghton Mifflin, 1962.

Conant, James B., et al, editors. *General Education in a Free Society.* Cambridge: Harvard University Press, 1945.

D'Arms, Eleonora, and Donald R. Griffin. "Balloonists' Reports of Sounds Audible to Migrating Birds." *The Auk*, Vol. 89, No. 2 (April 1972): 269-279.

Darwin, Charles. *The Expression of the Emotions in Man and Animals*. London: John Murray, 1872.

Davis, Hallowell, et al. "Further Analysis of Cochlear Activity and Auditory Action Currents: With Demonstration of Audible Response." *Transactions of the American Otological Society*, Vol. 23 (1933): 196-216.

Dawkins, Richard. *The Selfish Gene*, 30th Anniversary Edition. Oxford: Oxford University Press, 2006.

Dijkgraaf, Sven. "Over een merkwaardige functie van den gehoorzin bij vleermuizen [On a remarkable function of the sense of hearing in bats]." *Verslagen Nederlandsche Akademie van Wetenschappen Afdeeling Naturkunde*, Vol. 52 (1943): 622-627.

Fraenkel, Gottfried, and Donald Gunn. *The Orientation of Animals: Kineses, Taxes, and Compass Reactions*. Oxford: Oxford University Press, 1940.

Galambos, Robert, and Donald R. Griffin. "Obstacle Avoidance by Flying Bats: The Cries of Bats." *Journal of Experimental Zoology*, Vol. 89, No. 3 (April 1942): 475-490.

Galambos, Robert. "Cochlear Potentials Elicited from Bats by Supersonic Sounds." *Journal of the Acoustic Society of America*, Vol. 13 (July 1942): 41-49.

______. "The 1939-40 Bat Experiments that Validated Jurine's Claim." *Le Rhinolophe*, Vol. 11 (1995): 17-25.

______. "The Avoidance of Obstacles by Flying Bats: Spallanzani's Ideas (1794) and Later Theories." *Isis*, Vol. 34, No. 2 (1942): 132-140.

Gardner, R. Allen, and Beatrice T. Gardner. "Teaching Sign Language to a Chimpanzee." *Science*, Vol. 165, No. 3894 (August 1969): 664-672.

Glines, C.V. "Top Secret WWII Bat and Bird Bomber Program." *Aviation History*, Vol. 15 No. 5 (2005): 38-44.

Gould, James L. “Honey Bee Recruitment: The Dance-Language Controversy.” *Science*, Vol. 189, No. 4204 (August 1975): 685-693.

______. “Thinking about Thinking: How Donald R. Griffin Remade Animal Behavior.” *Animal Cognition*, Vol. 7 (2004): 1-4.

Gregg, Alan, et al, editors. *The Place of Psychology in an Ideal University*. Cambridge: Harvard University Press, 1947.

Griffin, Donald R. “Marking Bats.” *Journal of Mammalogy*, Vol. 15, No. 3 (August 1934): 202-207.

______. “Bat Banding: A Request for Cooperation.” *The Auk*, Vol. 53, No. 2 (April 1936): 253-254.

______. “Bat Banding.” *Journal of Mammalogy*, Vol. 17, No. 3 (August 1936): 235-239.

______. “Bats Migrate Too.” *New England Naturalist*, Vol. 5 (December 1939): 1-4.

______. “Wings without Feathers.” *New England Naturalist*, Vol. 3 (September 1939): 11-13.

______. “Homing Experiments with Leach’s Petrels.” *The Auk*, Vol. 57, No. 1 (January 1940): 61-74.

______. “Homing Experiments with Herring Gulls and Common Terns.” *Bird-Banding*, Vol. 14, No. 1/2 (1943): 7-33.

______. “Echolocation by Blind Men, Bats and Radar.” *Science*, Vol. 100, No. 2609 (December 1944): 589-590.

______. “How Bats Guide their Flight by Supersonic Echoes.” *The American Journal of Physics*, Vol. 12 (1944): 342-345.

______. “The Sensory Basis of Bird Navigation.” *Quarterly Review of Biology*, Vol. 19, No. 1 (March 1944): 15-31.

______. “Mystery Mammals of the Twilight.” *National Geographic*, Vol. 90 (July 1946): 117-134.

______. “The Supersonic Cries of Bats.” *Nature*, Vol. 158 (July 1946): 46-48.

______. “Measurements of the Ultrasonic Cries of Bats.” *Journal of the Acoustical Society of America*, Vol. 22 (March 1950): 247-257.

______. “The Navigation of Bats.” *Scientific American*, Vol. 138 (August 1950): 52-55.

______. “Acoustic Location of Insect Prey by Bats.” *Anatomical Record*, Vol. 111, No. 3 (1951): 448-449.

______. “At What Distance Can a Flying Bat Perceive Small Objects.” *Journal of Mammalogy*, Vol. 32, No. 4 (November 1951): 487-488.

______. “Airplane Observations of Homing Pigeons.” *Bulletin of the Museum of Comparative Zoology*, Vol. 107 (1952): 411-440.

______. “Bird Navigation.” *Biological Reviews*, Vol. 27 (1952): 359-390.

______. “Radioactive Tagging of Animals Under Natural Conditions.” *Ecology*, Vol. 33, No. 3 (July 1952): 329-335.

______. “Bat Sounds under Natural Conditions, with Evidence for Echolocation of Insect Prey.” *Journal of Experimental Zoology*, Vol. 123, No. 3 (August 1953): 435-465.

______. “Hearing and Acoustic Orientation in Marine Animals.” *Deep-Sea Research*, Vol. 3 (1953): 406-417.

______. “High Frequency Sounds of Tropical Bats.” *Anatomical Record*, Vol. 117 (1953): 567.

______. “Sensory Physiology and the Orientation of Animals.” *American Scientist*, Vol. 41, No. 2 (April 1953): 243-244.

______. “More about Bat ‘Radar.’” *Scientific American*, Vol. 199, No. 1 (1958): 40-44.

______. *Listening in the Dark: The Acoustic Orientation of Bats and Men*. New Haven: Yale University Press, 1958.

______. *Echoes of Bats and Men*. Garden City: Anchor Books, 1959.

______. *Bird Migration: The Biology and Physics of Orientation Behavior*. New York: Anchor Books, 1964.

______. “Echolocation and its Relevance to Communication Behavior.” In *Animal Communication*, edited by Thomas Sebeok, 154-164. Bloomington: Indiana University Press, 1968.

______. “Comments on Animal Sonar Symposium.” *The Journal of the Acoustical Society of America*, Vol. 54 (1972): 137-138.

______. “Oriented Bird Migration in or between Opaque Cloud Layers.” *Proceedings of the American Philosophical Society*, Vol. 117, No. 2 (April 1973): 117-141.

______. *The Question of Animal Awareness: Evolutionary Continuity of Mental Experience*. New York: Rockefeller University Press, 1976.

______. "Early History of Research on Echolocation." In *Animal Sonar Systems*, edited by Rene-Guy Busnel and J.F. Fish, 1-8. New York: Plenum Press, 1980.

______. *The Question of Animal Awareness*, 2nd edition. New York: Rockefeller University Press, 1981.

______. "Introduction." In *Animal Mind – Human Mind*, edited by Donald Griffin, 1-11. New York: Springer-Verlag, 1982.

______. *Animal Thinking*. Cambridge: Harvard University Press, 1984.

______. "Animal Consciousness." *Neuroscience & Biobehavioral Reviews*, Vol. 9 (1985): 615-622.

______. "Recollections of an Experimental Naturalist." In *Leaders in the Study of Animal Behavior*, edited by Donald Dewsbury, 120-142. Cranbury, NJ: Associated Universities Press, 1985.

______. *Animal Minds: Beyond Cognition to Consciousness*. Chicago: University of Chicago Press, 1992.

______. "[Autobiographical Memoir] Donald R. Griffin." In *History of Neuroscience in Autobiography,* Vol. 2, edited by Larry Squire, 68-93. San Diego: Academic Press, 1998.

______. "From Cognition to Consciousness." *Animal Cognition*, Vol. 1, No. 1 (July 1998): 3-16.

______. "Return to the Magic Well: Echolocation Behavior of Bats and Responses of Insect Prey." *BioScience*, Vol. 51, No. 7 (July 2001): 555-556.

Griffin, Donald R., J.H. Friend, and Frederick A. Webster. "Target Discrimination by the Echolocation of Bats." *Journal of Experimental Zoology*, Vol. 158, No. 2 (March 1965): 155-168.

Griffin, Donald R., and Robert Galambos. "The Sensory Basis of Obstacle Avoidance in Bats." *The Journal of Experimental Zoology*, Vol. 86, No. 3 (April 1941): 481-506.

Griffin, Donald R., and Alan D. Grinnell. "Ability of Bats to Discriminate Echoes from Louder Noise." *Science*, Vol. 128, No. 3316 (July 1958): 145-147.

______. “Neural Correlates of Echolocation in Bats.” *Federation Proceedings*, Vol. 17, No. 1 (1958): 61.

Griffin, Donald R., and Raymond J. Hock. “Experiments on Bird Navigation.” *Science*, Vol. 107, No. 2779 (April 1948): 347-349.

______. “Airplane Observations of Homing Birds.” *Ecology*, Vol. 30, No. 2 (April 1949): 176-198.

Griffin, Donald R., Ruth Hubbard, and George Wald. “The Sensitivity of the Human Eye to Infra-red Radiation.” *Journal of the Optical Society of America*, Vol. 37, No. 7 (July 1947): 546-554.

Griffin, Donald R., J.J.G. McCue, and Alan D. Grinnell. “The Resistance of Bats to Jamming.” *Journal of Experimental Zoology*, Vol. 152, No. 3 (1963): 229-250.

Griffin, Donald R., A. Novick, and M. Kornfield. “The Sensitivity of Echolocation in the Fruit Bat, Rousettus.” *Biological Bulletin*, Vol. 115, No. 1 (August 1958): 107-113**.**

Griffin, Donald R., Frederick A. Webster, and Charles R. Michael. “The Echolocation of Flying Insects by Bats,” *Animal Behaviour*, Vol. 8, No. 3-4 (1960): 141-154.

Griffin, Donald R. and John Welsh. “Activity Rhythms in Bats under Constant External Conditions.” *Journal of Mammalogy*, Vol. 18, No. 3 (August 1937): 337-342.

Griffin, Donald R., et al. “The Effects of Cold and Rate of Ascent on Aero-Embolism,” *Aviation Medicine*, Vol. 17 (February 1946): 56-66.

Grinnell, Alan, and Donald R. Griffin. “The Sensitivity of Echolocation in Bats.” *Biological Bulletin*, Vol. 114, No. 1 (February 1958): 10-22.

______. “The Neurophysiology of Audition in Bats.” *Anatomical Record*, Vol. 134, No. 3 (July 1959): 574.

Grinnell, Alan, and Verity Grinnell. “Neural Correlates of Vertical Localization by Echo-locating Bats.” *Journal of Physiology*, Vol. 181 (1965): 830-851.

Hachet-Souplet, Pierre. “Quelques experiences nouvelles sur les pigeons voyageurs.” *6th Congrès International de Psychologie* (1909): 663-673.

Hahn, Walter Louis. “Some Habits and Sensory Adaptations of Cave-Inhabiting Bats II.” *Biological Bulletin*, Vol. 15, No. 4 (September 1908): 165-193.

Hartridge, Hamilton. “The Avoidance of Objects by Bats in their Flight.” *Journal of Physiology*, Vol. 54, No. 1-2 (August 1920): 54-57.

Haskins, Caryl. “The Evolving Mind.” *Semiotica*, Vol. 23, No. 3 (1978): 381-385.

Hayes, Harvey C. “Detection of Submarines.” *Proceedings of the American Philosophical Society*, Vol. 59, No. 1 (1920): 1-47.

______. “U.S. Navy MV Type of Hydrophone as an Aid and Safeguard to Navigation.” *Proceedings of the American Philosophical Society*, Vol. 59, No. 5 (1920): 371-404.

Humphrey, Nicholas. “The Question of Animal Awareness.” *Animal Behaviour*, Vol. 25, No. 2 (1977): 521-522.

Hunt, Frederick V., editor. *Applied Acoustics in Subsurface Warfare* [Final Report of the Harvard Underwater Sound Laboratory, OSRD]. Cambridge, MA: Harvard Underwater Sound Laboratory, 1946.

Hutchinson, G. Evelyn. “Marginalia,” *American Scientist*, Vol. 36, No. 2 (April 1948): 218-222.

Johns Hopkins University. “Annual Report of the President, 1953.” In *Johns Hopkins University Circulars* (1952-53). MSEL Special Collections, Johns Hopkins University.

Kellogg, Winthrop N., Robert Kohler, and H.N. Morris. “Porpoise Sounds as Sonar Signals.” *Science*, Vol. 117, No. 3036 (March 1953): 239-243.

Kramer, Gustav. “Experiments on Bird Orientation.” *Ibis*, Vol. 94 (1952): 265-285.

Krogh, August. “The Language of the Bees.” *Scientific American*, Vol. 179 (August 1948): 18-21.

Lack, David, and R.M. Lockley. “Skokholm Bird Observatory Homing Experiments.” *British Birds*, Vol. 31 (1938): 242-248.

Lashley, Karl. “The Behavioristic Interpretation of Consciousness II.” *The Psychological Review*, Vol. 30, No. 5 (September 1923): 329-353.

______. “Experimental Analysis of Instinctive Behavior,” *Psychological Review*, Vol. 45, No. 6 (1938): 445-471.

______. “Persistent Problems in the Evolution of Mind.” *The Quarterly Review of Biology*, Vol. 24, No. 1 (March 1949): 28-42.

Lehrman, Daniel. “A Critique of Konrad Lorenz’s Theory of Instinctive Behavior.” *The Quarterly Review of Biology*, Vol. 28, No. 4 (December 1953): 337-363.

Lindauer, Martin. “Schwarmbienen auf Wohnungssuche.” *Zeitschrift für Vergleichende Physiologie*, Vol. 37 (1955): 263-324.

Loeb, Jacques. *The Mechanistic Conception of Life.* Chicago: University of Chicago Press, 1912.

Mason, William A. “Windows on Other Minds.” *Science*, Vol. 194, No. 4268 (November 1976): 930-931.

Matthews, G.V.T. “The Experimental Investigation of Navigation in Homing Pigeons.” *The Journal of Experimental Biology*, Vol. 28 (December 1951): 508-536.

______. “The Relation of Learning and Memory to the Orientation and Homing of Pigeons.” *Behaviour*, Vol. 4, No. 3 (1952): 202-221.

______. “Navigation in the Manx Shearwater.” *The Journal of Experimental Biology*, Vol. 30, No. 3 (1953): 370-396.

______. “Sun Navigation in Homing Pigeons.” *The Journal of Experimental Biology*, Vol. 30, No. 2 (1953): 243-267.

Maxim, Hiram. “The Sixth Sense of the Bat: Sir Hiram Maxim’s Contention. The Possible Prevention of Sea Collisions.” *Scientific American Supplement*, Vol. 74 (September 1912): 148-150.

Mayr, Ernst. “The Homing of Birds.” *Bird-Lore*, Vol. 39 (Jan.-Feb. 1937): 5-13.

Miller, George A. *The Psychology of Communication*. New York: Bantam Books, 1967.

Millikan, Robert A. “The New Opportunity in Science.” *Science*, Vol. 50, No. 1291 (September 1919): 285-297.

Morgan, Conwy Lloyd. *An Introduction to Comparative Psychology*. London: Walter Scott, 1896.

Nagel, Thomas. “What is It Like to be a Bat?” *The Philosophical Review*, Vol. 83, No. 4 (October 1974): 435-450.

Noyes, Atherton Jr., and George Washington Pierce. “Apparatus for Acoustic Research in the Supersonic Frequency Range.” *Journal of the Acoustic Society of America*, Vol. 9 (January 1938): 205-211.

Odum, Howard T. “The Bird Navigation Controversy.” *The Auk*, Vol. 65, No. 4 (October 1948): 584-597.

Parker, George H. "The New Harvard Biological Laboratories." *Science*, Vol. 76, No. 1964 (August 1932): 160.

Pepperberg, Irene. "Evidence for Conceptual Quantitative Abilities in the African Grey Parrot: Labeling of Cardinal Sets." *Ethology*, Vol. 75 (1987): 37-61.

Pierce, George Washington, and Donald R. Griffin. "Experimental Determination of Supersonic Notes Emitted by Bats." *Journal of Mammalogy*, Vol. 19, No. 4 (November 1938): 454-455.

Premack, David, and Ann James Premack. *The Mind of an Ape*. New York: Norton, 1983.

Reynaud, Gabriel. "The Orientation of Birds" [Translated], *Bird Lore*, Vol. 2, No. 4 (August 1900): 101-108.

Ristau, Carolyn, editor. *Cognitive Ethology: The Minds of Other Animals*. Hillsdale, NJ: Lawrence Erlbaum Associates, 1991.

Rowan, William. "Homing, Migration, and Instinct." *Science*, Vol. 102, No. 2643 (August 1945): 210-211.

______. "Experiments in Bird Migration." *Transactions of the Royal Society of Canada*, Vol. 40 (1946): 123-135.

Rüppell, Werner. "Heimfindeversuche mit Staren 1934." *Journal für Ornithologie*, Vol. 83, No. 3 (1935): 462-524.

______. "Heimfindeversuche mit Staren und Schwalben 1935." *Journal für Ornithologie*, Vol. 84, No. 2 (1936): 180-198.

______. "Heimfindeversuche mit Staren, Rauchschwalben, Wendehälsen, Rotrückenwürgern und Habichten [1936]," *Journal für Ornithologie*, Vol. 85, No. 1 (1937): 120-135.

______. "Ergebnis eines Heimfindeversuches mit aufgezogen Staren." *Vogelzug*, Vol. 9 (1938): 18-22.

Schneirla, T.C. "Bees." *Ecology*, Vol. 32, No. 3 (July 1951): 562-565.

Seyfarth, Robert, Dorothy Cheney, and Peter Marler. "Vervet Monkey Alarm Calls: Semantic Communication in a Free-Ranging Primate." *Animal Behaviour*, Vol. 28 (1980): 1070-1094.

Shannon, Claude. "A Mathematical Theory of Communication." *The Bell System Technical Journal*, Vol. 27 (1948): 379-423.

Shettleworth, Sara. “Cognitive Ethology and the Evolution of Mind.” In *Cognition, Evolution, and Behavior*, edited by Sara Shettleworth, 475-522. New York: Oxford Press, 1998.

______. “Do Animals Know That They Know.” *Trends in Cognitive Sciences*, Vol. 5, No. 9 (September 2001): 404-405.

Singer, Peter. *Animal Liberation: A New Ethics for Our Treatment of Animals*. New York: Random House, 1975.

Slepian, Joseph, Russell Varian, and Leverett Davis. “[Letters to the Editor] Remarks on ‘The Physical Basis of Bird Navigation.’” *The Journal of Applied Physics*, Vol. 19, No. 306 (March 1948): 306-308.

Stresemann, Erwin. “Haben die Vögel einen Ortsinn?” *Ardea*, Vol. 24 (1935): 213-226.

Supa, Michael, Milton Cotzin, and Karl Dallenbach. “‘Facial Vision’: The Perception of Obstacles by the Blind.” *The American Journal of Psychology*, Vol. 57, No. 2 (April 1944): 133-183.

Thomas, Roger K., and Rosanne B. Lorden. “Numerical Competence in Animals: A Conservative View.” In *The Development of Numerical Competence: Animal and Human Models*, edited by Sarah Boysen and E. John Capaldi, 127-147. Hillsdale, NJ: L. Erlbaum Associates, 1993.

Thomson, A. Landsborough. “Recent Progress in the Study of Bird-Migration: A Review of the Literature, 1926-1935.” *Ibis*, Vol. 27 (1936): 472-530.

Thorpe, William H. “Ising’s Theory of Bird Orientation.” *Nature*, Vol. 158, No. 4025 (December 1946): 903-904.

______. “Reductionism in Biology.” In *Studies in the Philosophy of Biology, Reduction, and Related Problems*, edited by Francisco J. Ayala and Theodosius Dobzhansky, 108-138. Berkeley: University of California Press, 1974.

Tolman, E.C. “Cognitive Maps in Rats and Men.” *The Psychological Review*, Vol. 55, No. 4 (July 1948): 189-208.

Viguier, Camille. “Le sens de l'orientation et ses organes chez les animaux et chez l'homme.” *Revue Philosophique de la France et de l'Etranger*, Vol. 14 (1882): 1-36.

Von Frisch, Karl. “Die ‘Sprache’ der Bienen und ihre Nutzanwendung in der Landwirtschaft.” *Experientia*, Vol. 2, No. 10 (1946): 397-404.

______. *Bees: Their Vision, Chemical Senses, and Language*. Ithaca: Cornell University Press, 1950.

Von Frisch, Karl, Adrian Wenner, and Dennis Johnson. "Honeybees: Do They Use Direction and Distance Information Provided by Their Dancers." *Science*, Vol. 158 (1973): 1072-1077.

Waring, Charles, editor. *Transmission and Reception of Sounds Under Combat Conditions: Summary Technical Report of Division 17*, Vol. 3. Washington DC: NDRC, 1946.

Watson, John B. "The Behavior of Noddy and Sooty Terns." *Papers from the Department of Marine Biology, Carnegie Institution of Washington* [Tortugas Laboratory Papers], Vol. 2, No. 103 (1908): 187-255.

______. "How Animals Find their Way Home." *Harpers Monthly Magazine,* Vol. 119, No. 713 (October 1909): 685-689.

______. "Psychology as the Behaviorist Views It." *Psychological Review*, Vol. 20, No. 2 (March 1913): 158-177.

Watson, John B., and Karl Lashley, "Homing and Related Activities of Birds." *Papers from the Department of Marine Biology, Carnegie Institution of Washington* [Tortugas Laboratory Papers], Vol. 7, No. 211 (1915): 1-104.

Whitaker, Arthur. "The Development of the Senses in Bats." *The Naturalist* (May 1906): 145-151.

Wilson, Edward O. *Sociobiology: The New Synthesis.* Cambridge: Belknap, Harvard University Press, 1975.

Wynne-Edwards, V.C. "Special Review: Yeagley's Theory of Bird Navigation." *Ibis*, Vol. 90, No. 4 (October 1948): 606-611.

Yeagley, Henry. "A Preliminary Study of a Physical Basis of Bird Navigation." *Journal of Applied Physics*, Vol. 18, No. 12 (December 1947): 1035-1063.

Secondary Sources

Allen, Colin, and Marc Bekoff. *Species of Mind: The Philosophy and Biology of Cognitive Ethology*. Cambridge, MA: MIT Press, 1997.

______. "Animal Minds, Cognitive Ethology, and Ethics." *The Journal of Ethics*, Vol. 11, No. 3 (September 2007): 299-317.

Allison, David K. "New Eye for the Navy: The Origin of Radar at the Naval Research Laboratory [NRL Report 8466]." Washington, DC: United States Government Printing Office, 1981.

Bardossi, Fulvio, and Judit N. Schwartz. "Sensible Animals." *Rockefeller University Research Profiles*, No. 23 (Winter 1985/86): 1-6.

Baxter, James P. *Scientists Against Time*. Boston: Little Brown, 1946.

Bekoff, Marc. "Cognitive Ethology and the Treatment of Non-Human Animals: How Matters of Mind Inform Matters of Welfare." *Animal Welfare*, Vol. 3 (1994): 75-96.

Boakes, Robert. *From Darwin to Behaviourism: Psychology and the Minds of Animals*. Cambridge: Cambridge University Press, 1984.

Bouyoucos, John V. "Frederick V. Hunt [Obituary]." *Physics Today*, Vol. 25, No. 7 (July 1972): 69-70.

Brink, Frank. "[Biographical Memoir of] Detlev Wulf Bronk," *Biographical Memoirs of the National Academy of Sciences of the United States* (1978): 1-87.

Brown, Louis. *Technical and Military Imperatives: A Radar History of World War II*. Philadelphia: Institute of Physics Publishing, 1999.

Buckley, Kerry W. *Mechanical Man: John Broadus Watson and the Beginnings of Behaviorism*. New York: The Guilford Press, 1989.

Burghardt, Gordon. "Animal Awareness: Current Perceptions and Historical Perspective." *American Psychologist*, Vol. 40, No. 8 (August 1985): 905-919.

Burkhardt, Richard. *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology.* Chicago: University of Chicago Press, 2005.

______. "Karl Ritter von Frisch." In *Complete Dictionary of Scientific Biography,* Vol. 17, edited by Charles Gillispie, 312-320. Detroit: Charles Scribner's Sons, 2008.

Cohen-Cole, Jamie. *The Open Mind: Cold War Politics and the Sciences of Human Nature.* Chicago: University of Chicago Press, 2014.

______. "The Politics of Psycholinguistics." *Journal of the History of the Behavioral Sciences*, Vol. 51, No. 1 (Winter 2015): 54-77.

Costall, Alan. "How Lloyd Morgan's Canon Backfired." *Journal of the History of the Behavioral Sciences*, Vol. 28 (April 1993): 113-122.

Crist, Eileen. "Griffin, Donald Redfield." In *Complete Dictionary of Scientific Biography,* Vol. 21, edited by Charles Gillispie, 177-186. Detroit: Charles Scribner's Sons, 2008.

Cronin, T.W., J. Marshall, and M. F. Wehling. "Talbot H. Waterman." *Philosophical Transactions of the Royal Society B*, Vol. 366, No. 1565 (March 2011): 617-618.

Crowther-Heyck, Hunter. "George A. Miller, Language, and the Computer Metaphor of Mind." *History of Psychology*, Vol. 2, No 1 (1999): 37-64.

Davis, Frederick. *The Man Who Saved the Sea Turtles*. Oxford: Oxford University Press, 2012.

Dennett, Daniel. *Consciousness Explained*. Boston: Little Brown, 1991.

Denny, Mark. *Blip, Ping, and Buzz: Making Sense of Radar and Sonar*. Baltimore: Johns Hopkins University Press, 2007.

Dethier, Vincent G. "Curiosity, Milieu, and Era." In *Studying Animal Behavior: Autobiographies of the Founders*, edited by Donald Dewsbury, 42-67. Chicago: University of Chicago Press, 1989.

Dewsbury, Donald. "A Brief History of the Study of Animal Behavior in North America." In *Perspectives in Ethology*, Vol. 8, edited by P.P.G. Bateson and P.H. Klopfer, 85-122. New York: Plenum, 1989.

______. "Americans in Europe: The Role of Travel in the Spread of European Ethology after World War II." *Animal Behaviour*, Vol. 49 (1995): 1649-1663.

Doherty, William H. "James Brown Fisk: 1910-1981." *Biographical Memoirs of the National Academy of Sciences of the United States.* Washington, DC: National Academies Press, 1987.

Edwards, Paul. *The Closed World: Computers and the Politics of Discourse in Cold War America*. Cambridge: MIT Press, 1988.

Elliott, Clark A. "Chronological Overview of Harvard Science (1636-1945) [Appendix 2]." In *Science at Harvard University*, edited by Clark A. Elliott and Margaret W. Rossiter, 331-360. Bethlehem: Lehigh University Press, 1992.

Farish, Matthew. "The Lab and the Land: Overcoming the Arctic in Alaska." *Isis*, Vol. 104, No. 1 (March 2013): 1-29.

Fletcher, Stephen H. "Harvey Fletcher: A Biographical Memoir." *Biographical Memoirs of the National Academy of Sciences of the United States*. Washington DC: National Academies Press, 1992.

Folk, G. Edgar. "The Harvard Fatigue Laboratory: Contributions to World War II." *Advances in Physiology Education*, Vol. 34, No. 3 (September 2010): 119-127.

Gray, Paul. "Harold E. Edgerton [Obituary]." *Physics Today*, Vol. 44 (1991): 126-128.

Greenwood, John D. "Understanding the 'Cognitive Revolution' in Psychology." *Journal of the History of the Behavioral Sciences*, Vol. 35, No. 1 (Winter 1999): 1-22.

Gross, Charles. "Donald R. Griffin." *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 86 (2005): 1-20.

Hankins, Thomas. "In Defence of Biography: The Use of Biography in History of Science." *History of Science*, Vol. 17, No. 1 (March 1979): 1-16.

Hollingsworth, J. Rogers. "Institutionalizing Excellence in Biomedical Research: The Case of The Rockefeller University." In *Creating a Tradition of Biomedical Research*, edited by Darwin H. Stapleton, 1-49. New York: The Rockefeller University Press, 2004.

Horvath, Steven M., and Elizabeth C. Horvath. *The Harvard Fatigue Laboratory: Its History and Contributions*. Englewood Cliffs, NJ: Prentice- Hall, 1973.

Isaac, Joel. *Working Knowledge: Making the Human Sciences from Parsons to Kuhn*. Cambridge: Harvard University Press, 2012.

Keller, Morton, and Phyllis Keller. *Making Harvard Modern: The Rise of America's University*. Cambridge: Oxford University Press, 2001.

Kennedy, John S. *The New Anthropomorphism*. Cambridge: Cambridge University Press, 1992.

Kobler, John. *The Rockefeller University Story*. New York: Rockefeller University Press, 1970.

Long, Tulley. “Constituting the Stress Response: Collaborative Networks and the Elucidation of the Pituitary-Adrenal Cortical System, 1930s-1960s.” Doctoral Thesis, Johns Hopkins University, 2011.

Miller, George A. “Stanley Smith Stevens: A Biographical Memoir.” *Biographical Memoirs of the National Academy of Sciences of the United States*. Washington DC: National Academies Press, 1975.

Mitchell, Robert, Nicholas Thompson, and H. Lyn Miles, editors. *Anthropomorphism, Anecdotes, and Animals*. Albany: SUNY Press, 1997.

Munz, Tania. “Of Birds and Bees: Karl von Frisch, Konrad Lorenz, and the Science of Animals, 1908-1973.” PhD diss., Princeton University, 2007.

______. “The Bee Battles: Karl von Frisch, Adrian Wenner and the Honey Bee Dance Language Controversy.” *Journal of the History of Biology*, Vol. 38 (2005): 535-570.

Pauly, Philip J. “The Loeb-Jennings Debate and the Science of Animal Behavior.” *Journal of the History of the Behavioral Sciences*, Vol. 17 (1981): 504-515.

______. *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology*. New York: Oxford University Press, 1987.

Peter Marler, “Hark Ye to the Birds.” In *Studying Animal Behavior: Autobiographies of the Founders*, edited by Donald Dewsbury, 314-345. Chicago: University of Chicago Press, 1985.

Radick, Gregory. *The Simian Tongue: The Long Debate about Animal Language*. Chicago: University of Chicago Press, 2007.

Raghuram, H., and G. Marimuthu. “The Discovery of Echolocation.” *Resonance*: *Journal of Science Education*, Vol. 10 (February 2005): 20-32.

Reed, John C., and Andreas G. Ronhovde. *Arctic Laboratory: A History of the Naval Arctic Research Laboratory at Point Barrow, Alaska*. Washington, DC: ONR, 1971.

Riggs, Lorrin A. “Carl Pfaffmann (1913-1994): A Biographical Memoir.” *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 71 (1997): 261-279.

Ristau, Carolyn. “Donald Redfield Griffin.” *Proceedings of the American Philosophical Society*, Vol. 149 (Sep. 2005): 399-411.

Romer, Alfred Shermer. “[Biographical Memoir of] George Howard Parker (1864-1955).” *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 53 (1967): 357-390.

Rose, Anne. “Animal Tales: Observations of the Emotions in American Experimental Psychology, 1890-1940.” *Journal of the History of the Behavioral Sciences*, Vol. 48, No. 4 (Fall 2012): 301-317.

Saunders, Frederick A., and Frederick V. Hunt. “[Biographical Memoir of] George Washington Pierce.” *Biographical Memoirs of the National Academy of Sciences of the United States*, Vol. 33 (1959): 351-380.

Shelesnyak, M.C. “Some Problems of Human Ecology in Polar Regions.” *Science*, Vol. 106, No. 2757 (October 1947): 405-409.

Smith, Roger. *Between Mind and Nature: A History of Psychology*. London: Reaktion Books, 2013.

Stapleton, Darwin. “Aspects of Instrumentation in the Neurosciences at Rockefeller University: Nobelists Herbert Gasser and H. Keffer Hartline.” Paper presented at the Annual Meeting of the International Society for the History of the Neurosciences, Los Angeles, California, June 20, 2007.

Stewart, Irving. *Organizing Scientific Research for War: The Administrative History of the Office of Scientific Research and Development*. Boston: Little, Brown and Company, 1948.

Thorpe, William H. *The Origins and Rise of Ethology: The Science of the Natural Behaviour of Animals*. London: Praeger, 1979.

Todes, Daniel. *Ivan Pavlov: A Russian Life in Science*. Oxford: Oxford University Press, 2014

Weidman, Nadine. *Constructing Scientific Psychology: Karl Lashley’s Mind-Brain Debates.* Cambridge: Cambridge University Press, 1999.

Winfree, Arthur T. *The Timing of Biological Clocks*. New York: Scientific American Books, 1987.

Young, Robert M. “Biography: The Basic Discipline for Human Science?” *Free Associations*, Vol. 11 (1985): 108-130.

CURRICULUM VITAE

Richard Stephen Nash, Jr. was born on May 23, 1982 in Oklahoma City, Oklahoma. He received his Bachelor of Arts in philosophy from Georgetown University in 2004. In 2012, he received his master's degree in the history of science from Johns Hopkins University. His master's thesis concerns debates over Darwinism, heredity, and evolutionary theory in the late-nineteenth century. Portions of his master's thesis were published as an article in *History and Philosophy of the Life Sciences* in 2015. His current area of focus is the history of evolutionary and behavioral biology, particularly animal behavior research in the late-nineteenth and twentieth centuries. He received a Johns Hopkins University Dean's Teaching Fellowship in 2015 to teach a course that he designed, "Animal Minds: Beyond the Black Box." He continued his academic work in 2016 with a postdoctoral fellowship at the Smithsonian Institution. His other interests include the history of capitalism, science and religion, biography, and American intellectual history.